Wild Orangutan Tool Use

NEW INSIGHTS FOR HUMAN EVOLUTION

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For all the great apes (human or non-human),
I have had the luck to know or meet
and be inspired by in one way or another…

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ABSTRACT

Tool use has traditionally been considered cognitively demanding and a hallmark of human evolution. However, the numerous findings of tool use across the animal kingdom have cast doubt on this notion. Using the existing variation among wild orangutans this thesis aimed to evaluate traditional evolutionary and cognitive theories on tool use.

I updated the tool catalogue for wild orangutans and evaluated in how far variation in extractive-foraging tendencies, intelligence, and opportunities for social learning explained the variation in tool repertoires within orangutans and of orangutans relative to chimpanzees (Chapter 2). I found that total, subsistence, and extractive-foraging tool variants were biased toward Sumatran orangutans and against Bornean orangutans. Among the Bornean orangutans, repertoire sizes were larger for *Pongo pygmaeus wurmbii* than for *Pongo pygmaeus morio*. Relative to wild orangutans, wild chimpanzee tool use was biased toward a greater number of total, subsistence, extractive-foraging, terrestrial and complex tool variants. Whereas the previously proposed socioecological model could not fully explain these findings, adding terrestriality to the model significantly improved its fit.

I further tested the terrestriality effect, hereafter referred to as terrestriality hypothesis, by evaluating four lines of comparative evidence among primates, which indeed supported the hypothesis (Chapter 3). First, the only monkey populations exhibiting habitual tool use and use of tool sets seem to be particularly terrestrial. Second, semi-terrestrial chimpanzees have more complex tool variants in their repertoire than do the arboreal orangutans. Third, tool variants of chimpanzees used in a terrestrial context tend to be more complex than those used exclusively in arboreal contexts. Fourth, the higher frequency in tool use among captive versus wild primates of the same species may be attributed in part to a terrestriality effect.

I hypothesized that terrestriality exerted its influence on tool repertoires through its positive effect on opportunities for innovation, manipulation, and tool-transfer interactions. The latter was tested by comparing the social context of tool use in chimpanzees and orangutans (Chapter 4). I found a higher tolerance of reactive transfers in terrestrial termite-fishing chimpanzees, relative to arboreal tool-using orangutans or chimpanzees. In the absence of proactive prosociality, such tool-transfer opportunities could indeed be crucial for the use of tool sets.

I, subsequently, reviewed ontogenetic and experimental studies on habitual tool use in animals in general, to assess whether their tool use is cognitively demanding and requires

social learning, in particular through tool-transfer interactions (Chapter 5). The ontogenetic process, with a late age of competence and influence of social-learning opportunities indeed indicated that habitual tool use is cognitively demanding and requires social-learning opportunities. However, whereas New Caledonian crows, capuchins and long-tailed macaques had opportunities for tool transfers, these were absent for bottlenose dolphins and orangutans, explaining perhaps their repertoires lack tool sets.

I evaluated whether orangutans use alternative strategies for acquiring tool use, which may tell us something about the cognitive demands underpinning orangutan tool use as well (Chapter 6). I found that habitual and flexible tool use in wild orangutans is cognitively demanding in that it requires a long time to acquire, including opportunities for social learning to stimulate initial tool-use attempts and to learn to recognize food resources.

I conclude that orangutan tool use may have an innate component but flexible use and manufacture needs to be learned and requires social-learning opportunities. Their arboreal and semi-solitary lifestyles may, however, have prevented wild orangutan populations from evolving more complex tool use, because social-learning through tool-transfer interactions facilitate routine use of more complex tool variants, such as seen for other habitual tool-using primates in the wild, captive orangutans and humans. I propose that opportunities for encountering artifacts facilitate cumulative culture, and probably played a crucial role during human (cognitive) evolution (Chapter 7).

ZUSAMMENFASSUNG (GERMAN ABSTRACT)

Werkzeuggebrauch wird traditionall als kognitiv anspruchsvoll und als Kennzeichen der menschlichen Evolution betrachtet. Allerdings stellen zahlreiche Erkenntnisse des Werkzeuggebrauchs innerhalb des Tierreichs diese Annahmen in Frage (Kapitel 1). In dieser Dissertation werden bestehenden Unterschiede zwischen wilden Orang-Utan Populationen in Borneo und Sumatra auf traditionell evolutionäre und kognitive Theorien über Werkzeuggebrauch untersucht.

Zuallererst wurden alle dokumentierten Nutzungen von verschieden Werkzeugen der Orang-Utans katalogisiert, damit deren Variation und Theorien im genaueren untersucht werden konnten. Anhand dieses Werkzeugkatalogs untersuchte ich, ob die sozial-ökologische Evolutionstheorie, mit extrahierender Futtersuche, Intelligenz und Möglichkeiten für soziales Lernen, die Variationen im Werkzeuggebrauch erklären kann. Dies untersuchte ich zum einen in verschieden Orang-Utan Populationen und zogen Vergleiche zu Schimpansen (Kapitel 2). Im Vergleich zu Borneo fand ich sowohl eine größere Variation bei verwendeten Werkzeugen, als auch eine größere Anzahl extrahierender Werkzeuge bei Orang-Utans aus Sumatra. Innerhalb der Orang-Utans aus Borneo war das Werkzeugrepertoire von *Pongo pygmaeus wurmbii* größer als das von *Pongo pygmaeus morio*. Im Gegensatz zu wilden Schimpansen jedoch verwenden wilde Orang-Utans sowohl weniger Werkzeugvarianten im Nahrungskontext, weniger "extrahierende Werkzeuge und fast keine terrestrischen und komplexeren Werkzeugvarianten. Das bisher vorgeschlagene sozial-ökologische Modell konnte diese Ergebnisse nicht vollständig erklären. Durch das Hinzufügen eines Terrestrialitätsfaktors konnte das Modell deutlich verbessert werden.

Das Phänomen, dass Terrestrialität die Komplexität von Werkzeug-varianten positiv beeinflusst, bezeichne ich in dieser Dissertation als "Terrestriality Hypothesis". Basierend auf dieser "Terrestriality Hypothesis" habe ich vier kategorische Annahmen kreiert, um folgende Hypothese zu testen: (1) regelmäßiger Einsatz von Werkzeugen geschieht in den Primatenpopulationen, die terrestrischer sind; (2) semi-terrestrische Schimpansen verwenden komplexere Werkzeugvarianten (d.h. ganze Werkzeug-Sätze "Tool-Sets") in ihrem Repertoire als in Bäumen lebenden Orang-Utans; (3) Werkzeugvarianten bei Schimpansen, die in einem terrestrischen Kontext verwendet werden, sind im allgemeinen viel komplexer als Werkzeugvarianten im arborealem Kontext; (4) arboreale Primartenarten in Gefangenschaft zeigen im Gegensatz zu ihren wilden Verwandten eine größere Vielfalt und mehr Variabilität im Werkzeuggebrauch, welches unter anderem mit der größeren Terrestrialität in

Gefangenschaft erklärt werden kann. In dieser Arbeit (Kapitel 3) konnte ich alle vier Annahmen und damit die "Terrestriality Hypothesis" bestätigen.

Ich vermute, dass Terrestrialität einen positiven Einfluss auf das Werkzeug Repertoire einer Population hat, durch erhöhte Chancen für Innovation, Manipulation und soziales Lernen. Im Zusammenhang des sozialen Lernens verglich ich den sozialen Kontext des Werkzeuggebrauchs zwischen wilden Schimpansen und Orang-Utans (Kapitel 4). Im Vergleich zu den baumlebenden Orang-Utans konnte ich häufigeren Werkzeugaustausch bei Schimpansen im terrestrischen (aber nicht im baumlebenden) Kontext feststellen. In Abwesenheit von selbst initiierter Prosozialität (d.h. proaktiver Werkzeug-Austausch) können solche Chancen für Werkzeug-Austausch entscheidend für die Verwendung von komplexeren Werkzeug Varianten (z.B. "Werkzeug-Sätze / "Tool-Sets") sein.

Anhand von schon bereits vorhandenen ontogenetischen und experimentellen Studien über habituellen (d.h. gewöhnlichen, aber nicht universellen) Werkzeuggebrauch im Tierreich habe ich zusätzlich Annahmen über die kognitiven Voraussetzungen und den Werkzeugerwerb überprüft (Kapitel 5). Werkzeugaustausch war erneut ein wichtiges Lernmittel für den Werkzeugerwerb bei den meisten habituellen Werkzeug verwendenden Tierarten (mit Ausnahme von u.a. dem Orang-Utan). Diese Tierarten sind dieselben, die auch komplexere Werkzeugsätze verwenden. Des Weiteren konnten ontogenetische Studien bestätigten, dass der Erwerb von habituellem Werkzeuggebrauch eine lange Lernzeit benötigt und dass der soziale Kontext ein Einfluss auf den Erwerb und die Ausführung hat. Daraus schliesse ich, dass habitueller Werkzeuggebrauch kognitiv anspruchsvoll ist und es hierfür soziale Stimmulierungen und Anreize benötigt.

Im Kapitel 4 und 5 erwähnte ich bereits, dass Werkzeug-Austausch beim den baumlebenden Orang-Utans abwesend ist. Somit untersuchte ich, ob die Orang-Utans eine alternative Strategie zum Werkzeuggebrauch und –erwerb verwenden und die Schlüsse, die ich durch den habituellen Werkzeuggebrauch bei wilden Orang-Utans in Bezug auf die kognitiven Voraussetzungen ziehen können (Kapitle 6). Auch hier deuten die lange Lernzeit und der Einfluss von sozialen Lernmöglichkeiten darauf hin, dass habitueller und flexibler Werkzeug-Einsatz bei wilden Orang-Utans kognitiv anspruchsvoll ist.

Ich schlussfolgere, dass Werkzeug-Gebrauch bei wilden Orang-Utans anspruchsvoll sein kann. Jedoch verhindert eine semi-solitäre Lebensweise und das Leben in den Bäumen (und deswegen weiniger Austausch Möglichkeiten), dass wilde Orang-Utans komplexerer Werkzeuge weiterentwickeln. Ich schlage deshalb vor, dass Gelegenheiten zum Werkzeugaustausch die Entwicklung von kumulativer Kultur erleichtert, was wahrscheinlich

eine entscheidende Rolle während der menschlichen (kognitiven) Evolution gespielt hat (Kapitel 7).

ABSTRAK (INDONESIAN ABSTRACT)

Penggunaan alat dipertimbangkan secara tradisional sebagai kompleks kognitif dan ciri khas evolusi pada manusia. Namun, sejumlah penemuan penggunaan alat pada hewan pada umumnya meragukan pernyataan ini. Oleh karena itu, disertasi ini disusun untuk mengevaluasi variasi teori kognitif dan evolusi tradisional penggunaan alat pada orangutan liar.

Pada disertasi ini, saya memperbaharui katalog penggunaan alat pada orangutan liar dan mengevaluasi bagaimana variasi pada ekstraksi untuk mendapatkan makanan, kecerdasan, dan kesempatan pembelajaran sosial (model sosial ekologi) yang menjelaskan perbendaharaan penggunaan alat diantara orangutan dan perbedaan orangutan dengan simpanse (Bab 2). Saya menemukan bahwa jumlah total penggunaan alat secara umum, alat mencari makanan dan alat ekstraksi untuk mendapatkan makanan pada orangutan sumatera lebih banyak dibandingkan pada orangutan borneo. Diantara orangutan borneo, ukuran perbendaharaan alat lebih banyak ditemukan pada *Pongo pygmaeus wurmbii* dibandingkan pada *P. p. morio*. Berbeda dengan orangutan, penggunaan alat oleh simpanse lebih banyak pada jumlah total penggunaan alat secara umum, alat mencari makanan, alat ekstraksi untuk mendapatkan makanan, alat yang digunakan secara terestrial, dan peralatan yang berfungsi secara khusus (bersifat kompleks). Namun, model sosial ekologi yang disebutkan diatas tidak dapat secara menyeluruh menjelaskan hasil penelitian ini sehingga penambahan faktor terestrial pada penelitian ini melengkapi model sosial ekologi.

Saya selanjutnya menguji hipotesa efek terrestrial dengan mengevaluasi empat kategori perbandingan pada primata yang mendukung hipotesa ini (bab 3). Pertama, satu-satunya populasi monyet yang menggunakan peralatan secara lokal (hanya ditemukan pada populasi tersebut) ditemukan saat mereka lebih banyak berada di permukaan tanah. Kedua, simpanse semi-terestrial menggunakan alat lebih kompleks dibandingkan orangutan arboreal. Ketiga, penggunaan alat pada simpanse di permukaan tanah lebih kompleks daripada penggunaan alat di atas pohon. Keempat, tingginya frekuensi penggunaan alat antara primata non-liar dan liar bergantung pada efek terrestrial.

Saya menyarankan adanya efek terrestrial pada perbendaharaan penggunaan alat yang bersifat positif untuk inovasi, manipulasi, dan penggunaan alat kembali oleh individu lainnya. Faktor terakhir ini teruji dengan membandingkan konteks sosial penggunaan alat pada orangutan dan simpanse (bab 4). Saya menemukan tingginya toleransi peralihan pada

penggunaan alat secara terestrial oleh simpanse yang dibandingkan dengan penggunaan alat secara arboreal oleh simpanse maupun orangutan. Tidak adanya pemberian alat proaktif dari satu individu ke individu lainnya menjadikan kesempatan untuk mendapatkan alat secara pasif dan reaktif sangat penting dalam menggunakan alat secara kompleks.

Saya kemudian mengulas studi perkembangan dan eksperimental pada hewan yang menggunakan alat secara lokal. Ulasan ini digunakan untuk mengevaluasi adanya penggunaan alat sebagai kompleks kognitif dan pembelajaran sosial khususnya melalui interasi peralihan alat (bab 5). Proses perkembangan membutuhkan waktu yang cukup lama dan dipengaruhi oleh kesempatan pembelajaran secara sosial. Hal ini mengindikasikan kompleks kognitif pada penggunaan alat secara local dan membutuhkan kesempatan pembelajaran sosial. Namun, ketidakadaan peralihan alat pada lumba-lumba dan orangutan menjelaskan kesederhanaan kompleksitas perbendaharaan alat mereka.

Saya mengevaluasi kemungkinan adanya strategi lain pada proses pembelajaran penggunaan alat untuk menjelaskan kompleks kognitif dalam penggunaan alat pada orangutan (Bab 6). Saya menemukan fleksibilitas penggunaan alat secara lokal pada orangutan liar membutuhkan waktu belajar yang cukup lama (termasuk kesempatan pembelajaran sosial). Pembelajaran sosial menstimulasi perilaku penggunaan alat untuk pertama kalinya dan belajar untuk mengenali sumberdaya makanan. Dari penemuan-penemuan ini saya menyimpulkan bahwa penggunaan alat pada orangutan merupakan kompleks kognitif.

Berdasarkan keseluruhan penelitian ini, saya menyimpulkan bahwa penggunaan alat pada orangutan sebagian diturunkan secara genetis, namun penggunaan alat secara fleksibel dan lokal membutuhkan kesempatan untuk belajar dan pembelajaran secara sosial. Pola hidup orangutan yang arboreal dan semi-soliter mungkin telah mencegah mereka untuk mengembangkan pola penggunaan alat yang lebih kompleks. Hal ini dikarenakan mereka tidak memiliki kesempatan untuk melakukan pembelajaran sosial melalui interaksi peralihan alat yang dibutuhkan untuk perkembangan kompleks perbendaharaan alat. Perkembangan kompleks perbendaharaan alat dapat ditemukan pada primata liar dengan penggunaan alat secara lokal, orangutan non-liar, dan manusia. Saya mengusulkan kesempatan untuk mendapatkan artefak yang memfasilitasi kumulatif budaya dan memainkan peran penting dalam evolusi (kognitif) manusia (Bab 7).

CHAPTER 1

General introduction

Tool use has long been thought of as a cognitive achievement and a hallmark of human evolution (Seed and Byrne 2010). However, the numerous fairly recent discoveries of adept tool use all over the animal kingdom have cast doubt upon the correctness of this view (Shumaker, Walkup et al. 2011). Research on how tool-assisted behaviors develop and evolve in a diverse mix of species is, therefore, a promising venue to shed light on how tool use might have become elaborated in humanity and to what extent it denotes advanced cognitive abilities. In particular, orangutans provide us with an interesting study model in this regard, because of their variation in tool use depending on the site or setting (i.e. wild vs. captive, Sumatra vs. Borneo, etc.), which in turn vary in the potential causal factors proposed to drive the evolution of tool use (van Schaik, Deaner et al. 1999; Wich, Utami-Atmoko et al. 2009). In this thesis, I will examine this variation among wild orangutans to test theories on the evolution and cognitive underpinnings of tool use and relate this to the cumulative technology advanced cognitive abilities we find in humans.

How to define tool use?

A first issue that needs to be dealt with, is how to define tool use. Often attempts to define "tool use" are elusive, somewhat subjective, and therefore controversial. The numerous definitions that have been proposed in the past all have their pro and cons (see Shumaker, Walkup et al. 2011 p. 1-6 for a review). In general the main critical aspects are *i)* whether or not objects need to be detached to be considered as tools (*e.g.* the use of a tree trunk as percussion substrate or bending a branch to reach fruits), *ii)* whether animate objects should be included (*e.g.* using conspecifics as social tools, using hosts as tools for reproduction by parasites, or the psychological use of conspecifics as tools in deception), *iii)* whether internally manufactured objects may count as tools (*e.g.* using a spider web to catch flies, faeces to chase away potential predators, or urine as a territorial marker), *iv)* whether tool use needs to be goal-directed (*e.g.* pressing the lever in a skinner box to obtain food), *v)* whether the use of a tool should increase efficiency (are cutlery and chopsticks as tools for eating

sometimes not even less efficient than using hands to eat? And what about tools for play?), *vi)* whether tool use may include goals other than feeding (*e.g.* self-maintenance such as the usage of water to wash body or mud to cool down), *vii)* what is the maximal latency between tool manipulation and reaching the goal (*e.g.* positioning a stick against a tree trunk on one day, and few months later climbing the tree by using this stick as a ladder), and *viii)* whether the tool manipulator needs to be identical to the individual reaching the goal (*e.g.* one individual drops a leaf in a tree hole with water, another takes the leaf, sucks out the water out and spits out the leaf wadge). Additional issues are *ix)* the use of water as tools, *x)* the inclusion of nest building as tool use, *xi)* tool use in play, and *xii)* incidental and thus potentially accidental use.

For the purpose of this thesis I follow the definition of Parker and Gibson (1977): "*the manipulation of an object (the tool), not part of the actor's anatomical equipment and not attached to a substrate, to change the position, action, or condition of another object, either directly through the action of the tool on the object or of the object on the tool, or through action at a distance as in aimed throwing*". I chose this definition because it seems most relevant when studying cognitive aspects of tool use and origins of human technology. This definition, furthermore, allows for comparison with studies on tool use performed in the past (e.g. Beck 1980). (See chapter three for a more elaborate argument and additional definitions on terminology related to tool use (*e.g.* tool manufacture, technology). Nevertheless, we need to remain aware that any definition will be arbitrary in excluding some but not other behaviors.

Did tool use make us human?

Modern humans depend on the use of tools in nearly all aspects of daily life, and tool use may reflect one of the most important adaptive shifts in human evolution. Whereas early hominins may have already relied on tools made from organic materials, Oldowan stone-tool technologies represent the first direct evidence for their tool use and manufacture. Dating back to around 2.5 Mya, these percussive technologies not only began to flourish almost simultaneously with the appearance of the genus *Homo*, they also coincided with the start of the increase in endocranial volume beyond the range of australopithecines and great apes, and represent the first hard evidence for human cultural behavior (Ambrose 2001).

However, Oldowan technologies may still have been within the limits of ape-grade adaptations, since also apes use tools to access and process food, discriminate and select raw materials to manufacture tools in advance of use, transport tools and food to repeatedly used activity areas, hierarchically and flexibly organize tool-related behavioral actions, show variation that appears to be cultural (Wynn, Hernandez-Aguilar et al. 2011).

The Acheulean technologies, appearing 1.76 Mya (Lepre, Roche et al. 2011) and characterized by large cutting tools, at some point (see Ambrose 2001 and references therein) started to surpass extant ape technologies by illustrating purposeful design rather than tool features imposed by the raw material. Such "shaping of tool material" reflect a capability for abstract thought that many assume has laid the foundation for modern human technology, social cognition, and cumulative culture at the beginning of the Upper Paleolithic period more than a million years later (Ambrose 2001; Plummer 2004; Stout 2011; Wynn, Hernandez-Aguilar et al. 2011; Pradhan, Tennie et al. 2012).

Is tool use cognitively demanding?

Tool use in natural settings by animals other than humans is restricted to a minority of animals (Bentley-Condit and Smith 2010), which probably contributes to the cognitive status of tool use. Nevertheless, tool use is widespread (i.e. found across at least three phyla and seven classes of the animal kingdom) and not only "intelligent" animals use tools (Beck 1980, p. 210; McGrew 1993, p. 167). A gradient with two extremes exists: tool use as a result of species-specific adaptations (extreme 1) and tool use that is the result of innovation or inhibition to adjust predisposed phenotypic biases according to the task or goal at hand (extreme 2) (Parker and Gibson 1977; Call 2013). Adaptations (extreme 1) require pre-existing behavior to evolve from (Parker and Gibson 1977; e.g. foraging on embedded resources: Kenward, Schloegl et al. 2011). Development is rather canalized (requiring little learning) and expression rather stereotypic and inflexible resulting in little to no variation among individuals, populations or contexts (Waddington 1942). Adjusting such adaptations to the task or goal at hand through inhibition or innovation is, however, indicative of more flexible problem-solving strategies that require learning and result in more phenotypic variation (Reader 2003; Easton 2005). Strong innovations (extreme 2) that are by definition harder to individually invent, may additionally require social inputs to become routine within the population (Coussi-Korbel and Fragaszy 1995; Tennie, Call et al. 2009). Phenotypic

variation in tools and contexts, individuals and populations, as well as the route of acquisition, may thus be indicative of innovative and flexible problem- solving capacities, and hence cognitive mechanisms underpinning tool use (see also chapter 4).

Among the small number of animal species that use tools in natural settings, almost 85% show tool use that is restricted to a single context, which probably points to extreme 1 as their developmental basis. The primate order seems to be the exception, in that about 35% of the tool-using species show tool use over at least three contexts, suggesting flexibility (extreme 2). The primate order, therefore, stands in sharp contrast to other groups, in which virtually no species shows such diverse uses of tools: mammalian orders (0%), Aves (2.4%), and Passeriformes (3.1%) (Bentley-Condit and Smith 2010).

Despite the behavioral similarities that unite the two extremes, tool use that is merely the result of species-specific adaptations (evolving from some pre-existing behavior) requires no cognitive abilities related to an understanding of the task or object relations (Call 2013; Hunt, Gray et al. 2013). Flexible tool use, however, may reflect a species' ability to adapt to new situations with novel solutions, which is cognitively demanding and seems to be a good proxy for advanced cognition (Reader 2003; Lefebvre, Reader et al. 2004; Easton 2005; Kaufman, Butt et al. 2011), and "intelligent human-like" tool use (Piaget 1952; Parker and Gibson 1977). Especially the need to systematically integrate multiple elements in a behavioral sequence is considered cognitively demanding, since it requires sustained attention, delayed achievement of the goal, and an understanding of the dynamic relationships between actions and objects (Tomasello and Call 1997; Byrne, Corp et al. 2001; Wulf and Shea 2002; Fragaszy, Visalberghi et al. 2004; Fragaszy 2007; Sanz and Morgan 2010; Boesch 2013). Although such hierarchical organization of behavior is not restricted to tool-assisted behaviors *per se* (see for example Byrne, Corp et al. 2001), tool-assisted behavior always includes an extra element to integrate in the behavioral scheme of actions, relative to when the same behavior is performed without tool (Parker and Gibson 1977; Sanz and Morgan 2010; Seed and Byrne 2010). Moreover, the general representation for using tools as an extension of the body, calls for different sensorimotor processing associated with neurological changes in the brain that are triggered by experience (Iriki 2006; Cook 2012). Last but not least, the ability to manipulate physical causality in a generalized manner by planning a complex sequence of actions to achieve a distant goal, is exactly what characterizes the more "human-like" tool use (Seed and Byrne 2010) (Parker and Gibson 1977) (Piaget 1952).

How orangutans can contribute to the study of tool use

I mentioned how the many findings of animal tool use may have served to confuse our perspective on tool use as a cognitive achievement and hallmark of human evolution. Similar enigmas exist for orangutan tool use on three levels. First, whereas captive and rehabilitant orangutans are known for their innovative and wide-range use of tools, that is at least as complex as that of chimpanzees, evidence for such elaborate tool use in wild orangutans remains scarce. The single tool catalogue reported for wild orangutans (which includes incidental tool use) documents only seven tool variants (Fox and Bin'Muhammad 2002). Furthermore, only two of these involve habitual and flexible tool use, which is found in only three populations.

Second, although among the great apes, orangutans are the least related to humans, they show similar cognitive abilities (Herrmann, Wobber et al. 2008) or may even outperform the other great apes (Lehner, Burkart et al. 2011; Manrique and Call 2011), (but see also Herrmann, Call et al. 2007; Manrique 2013). Orangutans, moreover, outperform gorillas and bonobos (but see Gruber, Singleton et al. 2012) in terms of their "intelligent human-like" tool use. Like chimpanzees, but in contrast to wild gorillas (Breuer, Ndoundou-Hockemba et al. 2005; Shumaker, Walkup et al. 2011) and bonobos (but see Gruber, Clay et al. 2010), orangutans are frugivorous, omnivorous, and extractive foragers with a large dietary repertoire consisting of many difficult-to-process food items. Extraction of embedded resources has been proposed as a selective force for the evolution of tool use either as adaptation (extreme 1) or as a more flexible problem-solving strategy (extreme 2) (Parker and Gibson 1977). However, some of the variation in tool use among primates remains unexplained with this purely ecological hypothesis (van Schaik, Deaner et al. 1999), including some of the intra-specific variation in orangutans (van Schaik and Knott 2001; van Schaik, Fox et al. 2003) and chimpanzees (Whiten, Goodall et al. 2001).

This leads us to the third reason for using orangutans as a model species to study the cognition and selective forces driving variation in animal tool use. Orangutans show extreme variation in the evolutionary factors proposed to drive the evolution of tool use (see more in chapter 2), which helps us to test these evolutionary theories. The clearest variation exists between the two species: the Sumatran "*Pongo abelii"* and the Bornean "*Pongo pygmaeus*", whose differentiation parallels ecological differences between the two islands they inhabit. There is a general trend for Sumatran forests to be more productive and less seasonal than Bornean forests, which could potentially have started a cascade of behavioral responses (*e.g.*

life-history pastes, foraging strategies, sociality, etc.) (Wich, Utami-Atmoko et al. 2009; van Schaik 2013). Additionally, the variation within islands allows us to examine the effect of an interaction of various socioecological factors (such as food availability and orangutan density or sociality).

Whereas, the numerous, potentially causal, differences between captive and wild orangutans are hard to untangle (e.g. social setting, enculturation, provisioning, free time, etc.), the variation between and within wild orangutan populations may thus enable us to test various evolutionary and ontogenetic scenarios proposed to explain the variation in tool use across primate species. This thesis may thereby provide us with more insight into factors driving the variation in tool use (including habitual, flexible and more cumulative tool use) among orangutans and between orangutans and chimpanzees. Ultimately, I hope this will provide us with more insight into the cognitive demands of tool use and the factors responsible for the elaborate technologies observed in captive orangutans, wild chimpanzees and humans.

Aims and contents of this study

By examining the variation within and between wild orangutan populations I aim to gain more insight in the selective pressures and cognitive demands associated with the evolution of tool use. For this I first need to update the orangutan tool catalogue and assess the existing variation, which is described in chapter 2. I try to find out what potential explanatory factors could be responsible for this variation within orangutans as well as between orangutans and chimpanzees. In chapter 3, I extrapolate the patterns and explanations I found in chapter 2 to primate tool use in general, to see if the patterns also hold there and can explain the variation across the primate order, as well as how these may relate to human evolution. In chapter 4 I compare the social context of tool use in chimpanzees and orangutans to find out in how far prosocial tendencies may relate to the patterns found in chapter 3. In chapter 5 I broaden our perspective to animal tool use in general, to see if the patterns found in chapter 3 and 4 also hold there. For this I focus on the species exhibiting habitual tool use since these are often considered to be intelligent. I evaluate this claim by reviewing longitudinal and experimental studies on the acquisition of habitually prevalent tool variants. In chapter 6, I apply this method to orangutans and use longitudinal data to evaluate whether also orangutan tool use may be cognitively demanding, and if so, what (alternative)

acquisition strategies they use relative. In chapter 7 I then synthesize our findings and examine how this thesis contributes to our understanding of the evolution and cognition of animal tool use and how these relate to cognitive and human evolution.

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CHAPTER 2

Orangutan tool use and the evolution of technology

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Introduction

Commonly referred to as a hallmark of human evolution, tool use is often considered a complex skill. Paradoxically, however, tool use seems to be widespread in the animal kingdom and may consist of fairly simple behavioral actions. In this chapter we try to relate these somewhat contradictory views to the relatively rare occurrence of habitual and complex tool use in wild orangutans, especially when compared to wild chimpanzees. We propose that, in addition to the previously suggested factors (i.e., extractive foraging, social tolerance and intelligence), terrestriality may have been instrumental in the evolution of especially habitual (*sensu* McGrew & Marchant, 1997) and complex tool use, thus explaining the "orangutan tool paradox." Our preliminary comparison of eight orangutan and ten chimpanzee study populations (descriptively, via a principal component analysis [PCA], and by testing predictions related to the four factors) does indeed point in this direction.

Defining tool use

Although tool use has been defined in various ways (see Shumaker *et al.*, 2011 for a detailed discussion), we choose to follow the definition of Parker and Gibson (1977): *Tool use is the manipulation of an object (the tool), not part of the actor's anatomical equipment and not attached to a substrate, to change the position, action, or condition of another object, either directly through the action of the tool on the object or of the object on the tool, or through action at a distance as in aimed throwing* (Modified from Parker & Gibson, 1977; Sanz & Morgan, 2007). We did not adopt the new definition proposed by Shumaker et al. (2011) because we believe that the criterion that objects are "not attached to a substrate" is very important. This condition may be particularly relevant for the evolution of complex tool

use, because detached objects can be more easily modified and can be incorporated more flexibly into tool combinations/sequences. We also avoided making inferences about an animal's intentions when using tools (e.g., to alter more efficiently the form, position or condition of another object, organism or the user itself: Beck, 1980). Therefore, Parker and Gibson's (1977) definition seems the most appropriate for this chapter.

Tool use as a reflection of a cognitive gradient

The significance of tool use lies in what it reveals about the cognitive abilities of its users. Although cognitive abilities may be reflected in many tasks, tool use provides us with the clearest window into the cognitive abilities underlying animal behavior (Byrne, 1995). This is not because tool use requires advanced cognition per se, but rather because of the cognitive gradient that can be recognized when animals use objects. This ranges from the fairly simple manipulation of fixed substrates or borderline tool use to true tool use in which objects are detached from their substrate (although use may still be stereotypic and inflexible); additional steps of manufacture and modification (Beck, 1980; Boesch & Boesch, 1990; McGrew, 1992; Bentley-Condit & Smith, 2010); flexible tool use, in which the tools are adjusted to the task at hand (van Schaik *et al.,* 1996); and finally accumulated tool use (also: cumulative or associated tool use), in which multiple innovations (cf. Reader & Laland, 2002) may be combined for a single purpose (Parker & Gibson, 1977; Beck, 1980; Byrne, 1995; Bentley-Condit & Smith, 2010; Shumaker *et al.,* 2011). Flexible and cumulative tool use in particular reveal the operation of intentions or mental simulation and planning, rather than direct responses to stimuli (Byrne, 1995), and therefore can be considered intelligent (Parker & Gibson, 1977).

Defining "complex" tool use

For this chapter we focus especially on the complex end of the tool-use gradient because of our interest in "the orangutan tool paradox": i.e., the rare occurrence of complex tool use in wild orangutans, although such complex tool use is fairly common for rehabilitant or captive orangutans (cf. van Schaik, 2004). Complex tool use has been defined in varying ways (Sanz & Morgan, 2010; Shumaker *et al.,* 2011). Here we define complex tool use as tool use that includes more than one element (accumulated), because the number of constituent elements will generally be correlated with the difficulty of learning and because hominin technology is characterized by increasing accumulation (cf. Haidle, 2010; Pradhan *et al.,* 2012). Where known, accumulated techniques are also generally accompanied by flexibility (adjustment to the task at hand) and acquisition through social learning (any kind of

learning that is triggered or influenced by other group members or conspecifics [cf. Fragaszy & Perry, 2003] and thus including also socially facilitated individual learning via, for example, stimulus enhancement). However, because these latter two aspects are less consistently reported in the literature, we focus on the accumulation criterion. This may not be perfect, in that some non-accumulated tool-use techniques may be cognitively challenging as well, but this is the most practical division of the complexity gradient.

Evolution of primate tool use

Apart from the insight it provides into cognitive abilities, tool use is also interesting from the perspective of human evolution. Among all tool-using taxa, primates are unique in the variation they show in tool-using contexts (Bentley-Condit & Smith, 2010). Nonetheless, habitual and complex tool use have often been considered a hallmark of hominins. Habitual tool use here refers to those tool-use variants that have been seen repeatedly in several individuals, consistent with some degree of social transmission (*sensu* McGrew & Marchant, 1997), excluding branch throwing in agonistic contexts, which is universal among primates. Within the primate order, only chimpanzees (McGrew, 2004b; Sanz & Morgan, 2007, 2009), orangutans (van Schaik *et al.,* 1996), some capuchins (Ottoni & Izar, 2008; Visalberghi *et al.,* 2009) and possibly some long-tailed macaques (Gumert *et al.,* 2009) are known to be capable of habitual tool use in natural conditions.

To explain the evolution of tool use in primates, van Schaik et al. (1999) proposed a socioecological model that includes a nested series of conditions. Tool use will be performed in broader contexts only when the primates engage in extractive foraging and are capable of dexterous manipulation (first two conditions). Species with more advanced innovative ability (intelligence) can also manufacture tools in both captivity and the wild (third condition). Subsequently, social tolerance allows for the spread of tool innovations within a population, allowing for habitual tool use and material culture (fourth condition). Finally, the ability for teaching in humans further allows for cumulative culture (fifth condition).

The potential role of terrestriality

Although the socioecological model explains the broad distribution of aspects of primate tool use, it cannot explain the rarity of complex tool use in all wild orangutans (van Schaik *et al.,* 1996) relative to chimpanzees (Whiten *et al.,* 2009). We would therefore like to propose to add terrestriality as a factor to the model. A terrestriality effect on tool innovations (especially for extractive foraging) and complex manipulations has already been

suggested in various previous studies (e.g., McGrew, 2004a; Visalberghi *et al.,* 2005; Humle & Matsuzawa, 2009; Spagnoletti *et al.,* 2009; but see Boesch-Achermann & Boesch, 1994). However, here we propose that terrestriality may not only affect opportunities for (complex) tool innovations, but may also affect opportunities for socially facilitated tool-affordance learning (*sensu* Huang & Charman, 2005), because previously used tools are more easily encountered in a terrestrial setting (see also Meulman *et al.,* 2012). Terrestriality may especially promote the occurrence and transmission of complex tool use, because accumulated technology is less likely to be invented independently and therefore relies more critically on propitious learning conditions. Orangutans are arboreal and appear to lack complex tool use. Thus, they provide us with an excellent opportunity to study the conditions favoring the origins of complex tool use, and hence the foundation of hominin cumulative technology.

Orangutans

Among the great apes, orangutans are the least related to humans. The current con*sensu*s among paleoanthropologists is that the orangutan lineage and that of the other great apes separated around 14 Mya (Kelley, 2002; Raaum *et al.,* 2005). Today, orangutans are only found on the islands of Sumatra and Borneo, in Southeast Asia. They are commonly subdivided into two species, the Sumatran *Pongo abelii* and the Bornean *Pongo pygmaeus* (Xu & Arnason, 1996; Warren *et al.,* 2001). The existing taxonomic subdivision of the three Bornean subspecies (*P. p. pygmaeus, P. p. wurmbii* and *P. p. morio*), described on the basis of morphological characteristics (Groves, 2001), however, does not adequately capture the genetic variation within this species (Arora *et al.,* 2010).

Orangutans are large-bodied great apes that live in habitats varying from coastal peat swamp forest to montane dryland rainforest. They mainly differ from the African great apes in that females are almost exclusively arboreal, and, despite variation in gregariousness across populations, are generally semi-solitary. Bornean males are more terrestrial, but almost exclusively solitary apart from brief consortships with females (Utami-Atmoko *et al.,* 2009).

Ecologically, orangutans are much like chimpanzees, being frugivorous and omnivorous foragers with a large dietary repertoire. This includes extractive foraging, which means that they extract food items from the matrices in which these items are embedded. Orangutans feed, for example, on seeds of *Polyalthia glauca* after first discarding the foul-tasting pulp, and remove the seeds of *Neesia* sp. without even touching the prickly matrix embedding them. Insects or their products (e.g., honey, larvae) are extracted from nests that

are often located in tree holes, or picked up after pulling bole climbers off the trunk. Pith is extracted from hearts or stems of palm trees or the young twigs of *Dyera costulata*, and tree cambium is scraped off inner bark after first removing the outer bark of tree trunks. Because all these items are embedded in a matrix that is hard, or even dangerous, animals must learn to identify them as food and overcome their defenses. This strong reliance on extractive foraging leads us to expect abundant tool use in orangutans.

This study

Updating the orangutan tool catalog

In this chapter we have compiled all available information on wild orangutan tool use to create an updated overview of the orangutan tool repertoire and to compare this to the chimpanzee tool repertoire. To allow for fair comparison, and to exclude effects such as enculturation that are less directly relevant for understanding the occurrence and evolution of tool use in primates, only wild populations were considered.

Describing the variation in tool repertoires

To establish the main components distinguishing tool repertoires across sites, and to gain insight into the level of interdependency between outcome variables, one can conduct a PCA. Eight outcome variables (or nine when we included nest variables – see discussion) were included as a potential source of variation in the tool repertoires. These included three context-related variables to help us to better discriminate between different aspects of the tool repertoire and innovation biases that may exist. Based on the socioecological model of van Schaik et al. (1999) we expect the following outcome variables to cluster together: (1) intelligence – physical comfort tool variants (non-extractive), total number of tool variants, complex tool variants; (2) extractive foraging – extractive foraging tool variants, subsistence tool variants, total number of tool variants; (3) social tolerance – cultural tool variants, communication tool variants, total number of tool variants. However, if we include the potential terrestriality effect, we expect terrestrial, extractive, cultural, complex, subsistence, communication and the total number of tool variants to cluster together because of the potential positive effect of terrestriality on extractive foraging, social learning and the acquisition of complex skills. The second component should then include physical comfort tool variants and the total number of tool variants.

Predictions of the new model

To gain some insight into the independent effects of each of the four predictor variables on the variation in tool repertoires across sites and the importance of interactions between predictor variables, a multiple regression analysis would have been ideal. Sample size, however, did not allow for a multiple regression analysis to predict the best explanatory model for each component extracted from the PCA. We decided to use bivariate analysis as an alternative method for testing the predictions regarding the effects of the four factors on the tool repertoires of the various orangutan and chimpanzee populations. Although these analyses ignore possible interaction effects among the factors, we believe they do help us understand the extent of the direct effects of the four factors on the tool repertoire. Hence, although preliminary, these results should give us an idea of the best explanatory model for the variation in tool repertoires.

We will now discuss the proxies used for each factor and develop predictions for the expected differences among orangutan populations and between orangutans and chimpanzees.

Testing the role of intelligence

Intelligence can be viewed as general cognitive ability (Deaner *et al.,* 2007; Reader *et al.,* 2011). Although the best proxy measure of such general cognitive abilities or intelligence is still highly debated, these studies showed that absolute measures of brain size provided a far better fit than body-size-corrected measures such as the encephalisation quotient. We therefore considered absolute correlates of cranial capacity to be a valid proxy for intelligence, especially given that female great apes are quite similar in body size. An additional advantage of taking this measure is that it allows us to compare the different orangutan species and subspecies.

For females, cranial capacity is almost identical between chimpanzees and orangutans (Isler *et al.,* 2008). Among orangutans, however, *P. p. morio* (northeast Borneo) have significantly smaller cranial capacities than the Sumatran orangutans (*P. abelii*), with *P. p. wurmbii* (central Kalimantan/southern Borneo) being intermediate but closer to *P. abelii* (Taylor & van Schaik, 2007). We therefore considered *P. p. morio* somewhat less intelligent than the other orangutan subspecies (although this has not been formally tested). Nevertheless, we also report the results when *P. p. morio* were included in the analyses. We expected no differences between chimpanzees and (non-*morio*) orangutans in general (see also Deaner *et al.,* 2007; Reader *et al.,* 2011).

The prediction is that innovative ability, as proxied by intelligence, predicts total tool repertoire size (see also Reader & Laland, 2002). However, the latter may be confounded by other variables. First, given the known variation in reliance on extractive foraging, a cleaner estimate of the role of intelligence would be to examine the repertoire size of tool variants not used for extractive foraging. Second, variation among populations and species in opportunities for social learning may affect the likelihood that innovations persist. Thus, it is possible that the total repertoire is greater in species or populations with better opportunities for social learning (van Schaik, 2006). Hence, tool complexity may be a better measure of intelligence, although it in turn may be affected by terrestriality and opportunities for social learning (see below). We will therefore use the total repertoire of non-extractive tool variants and tool complexity as preliminary estimates of the effect of intelligence (Table 9.1).

Table 9.1 Predicted differences in tool repertoire between orangutan populations and between orangutan and chimpanzee populations, depending on the potential terrestriality effect.

Role of	**Measure**	**Kind of tools**	**OU-B vs. S**	**OU vs. CH (−Terrestriality)**	**OU vs. CH (+Terrestriality)**
Intelligence	Cranial capacity	Non-extractive	B(m) < B, S (nm)	OU(nm)= CH	OU(nm) ≤ CH
		complex	B(m) < B, S (nm)	OU(nm)= CH	OU(nm)<CH
Extraction	Insectivory	Extractive	B (nm) < S	OU(nm) = CH	OU(nm)< CH
Opportunities for social learning	Social tolerance	Cultural	B (nm) < S	OU(nm) < CH	OU(nm)<<CH

Notes

B = Bornean orangutans, S = Sumatran orangutans, m = *morio*,nm = non-*morio*, OU(nm)= non-*morio* orangutans, CH = chimpanzees, −/+Terrestriality: ex-/including potential terrestriality effect, respectively. The first three columns describe what has been tested, the last three columns describe the predictions for each comparison and test. For orangutans the ex-or inclusion of the potential terrestriality effect has no effect on the predictions.

Testing the role of extractive foraging

Currently few quantitative estimates for extractive foraging frequency exist. The effect of extractive foraging opportunities is best estimated by comparing the total repertoire of extractive tool variants. As almost all insectivory is extractive, insectivory may be the best proxy for estimating tendencies toward extractive foraging (van Schaik *et al.*, 1999). This is especially likely since other extractive activities are not amenable to support tool use (e.g., the extraction of cambium or bark by Bornean orangutans). Nevertheless, to validate this, we need to establish that most insect foraging is indeed extractive. Data confirm this (Tuanan: >95%, M. A. van Noordwijk, 2010, unpublished data; Suaq Balimbing: >75%, Sitompul,

1995). Overall, Sumatran orangutans are more insectivorous than Bornean orangutans (11% of the total feeding time in Sumatran populations, about 5.7% for *P. p. wurmbii* and ca. 1.4% for *P. p. morio*) (Morrogh-Bernard *et al.,* 2009). It is commonly thought that chimpanzees rely more on extractive foraging than orangutans. However, the mean percentage of insectivory across chimpanzee populations is around 4% (Stumpf, 2007), similar to Bornean orangutans. Thus, until future work provides better estimates of the incidence of extractive foraging, it is parsimonious to expect that Sumatran orangutans have more extractive foraging tool variants than Bornean orangutans, but that there are no systematic species differences between the two great ape species (see Table 9.1).

Testing the role of social tolerance

Opportunities for social learning will depend on the degree of tolerant proximity (Coussi-Korbel & Fragaszy, 1995). Among orangutans, Sumatran populations are much more gregarious than the Bornean populations (van Schaik, 1999; van Noordwijk *et al.,* 2009), largely due to differences in forest productivity and food availability (van Schaik, 1999; Marshall *et al.,* 2009). Most chimpanzee populations are more gregarious than orangutans (van Schaik *et al.,* 2003c). Thus, chimpanzees have more opportunities for social learning than orangutans, and Sumatran orangutans have more than Bornean orangutans. The size of the cultural tool repertoire is usually considered to be a good estimate for the effect of opportunities for social learning (see Table 9.1).

Testing the role of terrestriality

The increased innovation tendencies are expected to primarily affect the number of (terrestrial) extractive tool variants. Moreover, as explained above, enhanced social learning opportunities should increase the number of complex tool variants within the repertoire more than the simple forms. We therefore predict that the socially tolerant terrestrial chimpanzees have more extractive (cultural) and complex (cultural) tool variants in their repertoire than the semi-solitary arboreal orangutans. This contrasts with the predictions of the socioecological model (see Table 9.1). Moreover, we expect that tools used on the ground are more complex than tool variants used in arboreal settings. Because orangutans are rarely terrestrial and usually solitary (aside from consortships), we expect no differences in tool complexity between the various orangutan populations due to terrestriality (Table 9.1).

Methods

Orangutan tool catalog

Despite the recent wave of interest in innovation and culture in orangutans, so far no complete tool catalogs have been compiled for wild orangutans (but see Fox & Bin'Muhammad, 2002). We therefore reviewed the literature on tool use, innovations and culture in wild orangutans (Russon *et al.,* 2009; van Schaik *et al.,* 2009), and added some unpublished observations from Suaq Balimbing, to construct a tool-use inventory for eight wild orangutan populations in Sumatra and Borneo (Figure 9.1). We trust that this provides us with the complete tool repertoire for orangutans at existing study sites (especially for the habitual tool variants), because tool-use behaviors are striking to observers and have been a focus of attention for at least three decades (van Schaik *et al.,* 1996; Fox & Bin'Muhammad, 2002).

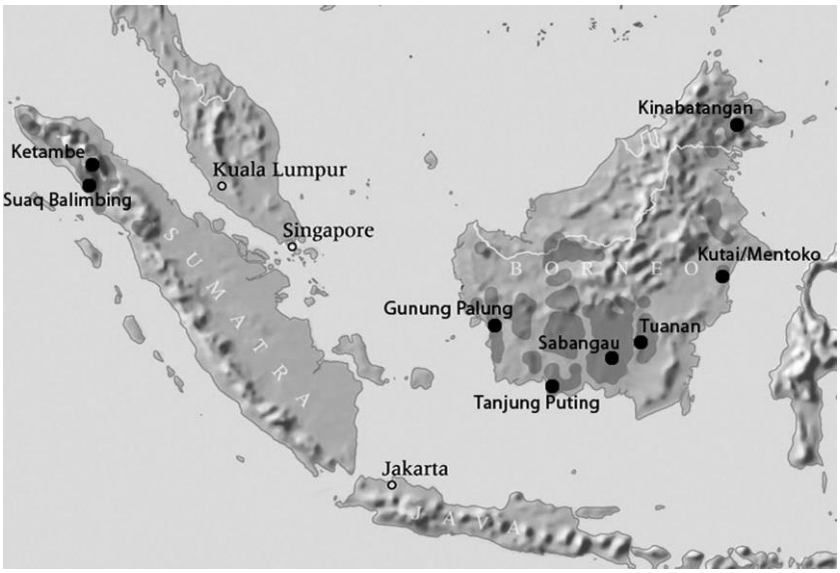

Figure 9.1 Map showing the locations of the eight orangutan study sites (black dots) that have been included in the tool catalog. Dark-shaded areas indicate orangutan distribution.

Chimpanzee tool catalog

For the species comparison to chimpanzees we used the chimpanzee tool repertoire as reported by Sanz and Morgan (2007). We additionally included one new tool variant reported for Goualougo –"ant nest perforation" (Sanz *et al.,* 2010). For information about cultural status, tool complexity and terrestrial use, see Meulman et al. (2012).

Criteria for the inclusion of tool variants in the tool catalog

To be able to compare orangutan tool repertoires with those of chimpanzees, we applied the same criteria for the inclusion of tool variants as reported by Sanz and Morgan (2007) (see also Whiten *et al.,* 2001). Hence, dependent on the similarity of the action patterns, tool variants were split or lumped. Similar criteria have been reported in the literature on cultural behavioral variants in wild orangutans (van Schaik *et al.,* 2003a; Wich *et al.,* 2009).

"Accidental" innovations reflect the potential for innovation and flexible and complex tool use, and have also been included in the chimpanzee tool catalog described by Sanz and Morgan (2007). We therefore included them here as well to facilitate unbiased comparisons. For the same reason, we excluded objects for which or use in play could not be excluded, as well as nest elements, given that nest-building activities are generally not considered as tool use (Beck, 1980). We will nonetheless discuss nest-building elements, since we think that some involve true tool use (i.e., nest pillow, nest blanket, nest lining, nest roof, artistic pillow), and are important from a cognitive and evolutionary perspective (see discussion).

Classification of tool variants

The most basic measure for the variation in tool repertoire across sites is the total repertoire of tool variants for a given population. All tool variants in the tool catalog were subsequently evaluated in terms of their classification as extractive foraging, cultural, complex and terrestrial; and their context use in terms of subsistence, physical comfort or communication.

A subset of the total tool repertoire is the repertoire of tool variants used for extractive foraging: tool variants used to extract an edible item from an inedible matrix. Based on this definition, tools used to obtain water from tree holes (e.g., sponging) were considered extractive foraging tool variants, whereas tools used to obtain water from ponds or streams were not (e.g., algae scoop).

Another subset is the cultural tool repertoire of a population. We identified putative cultural tool variants as those behavioral patterns that are absent without ecological explanation in at least one community, yet achieve at least habitual status in at least one other community, excluding those that are species universals (i.e., at least habitual prevalence observed at each site and therefore thought to have more canalized development) (Whiten *et al.,* 1999). This approach has recently been validated for orangutans (Krützen *et al.,* 2011).

A fourth measure is the complexity of the tool variants. We classified tool variants as

complex when the accumulation of tools, including the particular tool variant (e.g., in tool sets or combined tool use *sensu* McGrew, 2010), has been reported in the literature.

Tool variants may be used exclusively in arboreal conditions or in terrestrial conditions as well (a fifth measure or outcome variable). They can furthermore be classified according to the context in which they were used (*sensu* van Schaik *et al.*, 2006): subsistence, physical comfort and communication (outcome variables 6–8). In instances of doubt, tool variants were classified according to their direct purpose. Hence, tooth-cleaning tools, for example, were classified as physical-comfort tool variants because they were not used to assist feeding but used after feeding to enhance physical comfort or hygiene. Where multiple contexts were possible, we chose the predominant one (e.g., a branch swatter is mainly used to protect against insects while resting, but can also assist in feeding on bees' nests).

Statistical analysis

Given the small sample sizes, we used (if possible) non-parametric statistical tests with exact p-values (two-tailed), and also reported trends. The repertoires of the three orangutan subspecies were compared with the Kruskal–Wallis test. Mann–Whitney U tests were used to compare orangutan with chimpanzee repertoires. The distribution of tool variants over the three behavioral contexts was tested with a Chi-square over the 81 tool variants (chimpanzees: n = 43, orangutans: n = 38).

We conducted a PCA with orthogonal rotation (varimax) to extract the factors relevant for distinguishing tool repertoires of different study sites, and to look at the clustering of the various subsets of tool variants. Bivariate correlation analyses were conducted to test the effect of study duration on the eight outcome variables included in the PCA.

To test the effect of the four factors proposed to be relevant for the evolution of tool use, populations and (sub)species were compared with the Mann–Whitney U test by taking the mean number of tool variants per long-term study site, to control for sampling intensity (chimpanzees: n = 10; *P. p. wurmbii*: n =4; *P. p. morio*: n = 2; and *P. abelii*: n =2 study sites). Furthermore, we performed Mann–Whitney U tests to evaluate whether complex tool variants differed from simple tool variants recorded for orangutans and chimpanzees (total n = 81) in being used more terrestrially and/or extractively.

Results

Tool catalogs

For wild orangutans a total of 38 (true) tool variants (excluding five nest-building variants that could also be considered true tool use) have been reported (see Table 9.2). This number includes a hitherto unpublished variant, the "straw tool": using a tool to drink water from a tree hole or hole in the liana bark (n = 3 observations). The entire catalog included seven tool variants used for extractive foraging (amounting to 18% of the total repertoire); 16 tool variants that were potentially cultural (42%); two (5%) were used in terrestrial contexts; and zero variants contained multiple elements and hence were considered complex. All five nest elements (not included in the above-mentioned totals) were classified as non-cultural, complex, physical-comfort tool variants. Regarding the context, 13 (34%) of the orangutan tool variants were used in the subsistence context, 18 (47%) for physical comfort and 7 (18%) for communication.

Figure 9.2 shows the distribution of tool variants over the eight wild orangutan study sites included in the analysis. The figure indicates that differences regarding the number of tool variants between the subspecies are all in favor of *P. abelii*, against *P. p. morio*, with P. *p. wurmbii* being intermediate. Only the total number of tools differed significantly among the three subspecies ($\chi^2(2) = 6.1$; $p = 0.014$), whereas a trend was observed for the number of extractive tool variants: $\chi^2(2) = 5.1$; $p = 0.057$. The number of complex, cultural, subsistence, physical-comfort and communication tools did not differ significantly among the subspecies. A bivariate correlation analysis revealed no significant correlation of study duration with any of the eight outcome variables.

The chimpanzee catalog included 43 variants, including 23 (53%) extractive, 17 (40%) complex, 23 (53%) cultural and 32 (74%) terrestrial tool variants. With regard to the context, 26 (60%) of the chimpanzee tool variants were used for subsistence, 12 (28%) for physical comfort and 5 (12%) for communication. Sanz and Morgan (2007) also reported that study duration did not significantly affect total or cultural (as defined here) tool repertoires.

In contrast to the species-wide total numbers mentioned above, we used average numbers per site to compare (sub)species and populations to ensure a fair comparison with the comparative data within orangutans. Figure 9.3 shows the tool repertoire size, and the number of extractive-foraging, cultural, complex and terrestrial tool variants (Figure 9.3a), as well as the number of subsistence, physical-comfort and communication tool variants (Figure 9.3b), for orangutans compared with chimpanzees.

Table 9.2 Orangutan tool catalog. An overview of all the tool variants (and nest elements) reported for wild orangutans; comparing their prevalence across eight long-term orangutan study populations.

				Study sites									
Tool variant	**Cont.**	**EF**	**Cult.**	***GP***	***TP***	***SA***	***TU***	***KU***	***KI***	***KE***	***SB***	**Ref**	**Source**
Leaf bundle ("doll")	2	0	0	R	R	A	R	A	A	R	A	1	T 21.2, 20.1
Auto-erotic tool	2	0	1	A	A	A	A	P	A	C	A	1	T 21.1, 20.1
Bee cover	2	0	0	A	A	A	R	A	P	P	R	1-3	T 21.2, 20.1
Branch cushion	2	0	1	R	H	H	C	?	A	H	C	1,3	T 21.1, 20.1
Branch hide	3	0	0	A	R	A	A	P	R	R	R	1-3	T 21.2, 20.1
Branch hook	2	0	0	A	A	R	R	?	A	?	R	1,3	T 21.2, 20.1
Branch reach fruit	1	0	0	A	R	A	A	A	A	A	A	2	
Branch scoop	1	1	1	A	A	H	A	A	A	A	H	1	T 21.1, 20.1
Branch as swatter	1	0	1	R	R	R	A	H	H	H	H	1	T 21.1, 20.1
Branch fan	2	0	0	?	?	?	?	?	?	?	?	2	
Branch dragging display	3	0	0	A	A	A	A	?	R	E	E	1	T 21.2, 20.1
Foam leaf body	2	0	1	A	A	H	A	?	A	A	A	1	T 21.1, 20.1
Club	3	0	0	R	A	A	A	A	A	A	A	2	
Leaf wipe	3	0	1	A	C	A	A	A	A	A	R	1,3	T 21.1, 20.1
Kisssqueak leaves	3	0	1	C	A	R	H	H	A	R	R	1,3	T 21.1, 20.1
Leaf cushion	2	0	1	E	R	E	E	A	R	C	A	1,3	T 21.1, 20.1
Leaf glove (bite)	1	0	0	A	A	R	A	?	?	R	A	1,2	T 21.2, 20.1
Leaf glove (spine)	1	0	1	E	R	E	E	A	R	H	A	1,3	T 21.1, 20.1
Leaf napkin	2	0	1	A	A	A	A	C	A	R	R	1,3	T 21.1, 20.1
Poultice use	2	0	0	A	A	R	A	?	A	A	A	1	T 21.2, 20.1
Leaf scoop	1	0	0	R	A	A	A	A	A	A	A	1	T 21.2, 20.1
Sponging	1	1	0	A	A	R	A	A	A	R	A	1	T 21.2, 20.1
Moss cleaning	2	0	1	A	A	H	A	?	A	A	A	1	T 21.1, 20.1
Leaf wiper	2	0	0	R	A	R	A	A	A	A	A	1	T 21.2, 20.1
Aimed missile	3	0	0	C	C	C	C	C	C	C	C	2	
Nail cleaning	2	0	0	?	A	A	A	?	?	P	A	1	T 21.2, 20.1
Hat cover	2	0	0	C	C	C	C	C	C	C	C	1,2	T 21.2
Scratch with stick	2	0	1	A	R	R	R	H	A	A	A	1	T 21.1, 20.1
Snag crash	3	0	0	C	C	C	C	C	C	C	C	1	P 21.3.3
Snag riding	2	0	1	A	C	R	H	A	A	A	R	1,3	T 21.1, 20.1
Stick as chisel (1-Nest)	1	1	0	A	R	A	A	A	A	R	A	1	T 21.2, 20.1
Stick as chisel (2-Durian)	1	1	0	A	A	A	E	A	A	R	A	1	T 21.2, 20.1
Stick push spine	1	0	0	A	A	A	E	?	A	R	A	2	
Seed-extraction tool use	1	1	1	A	A	E	E	E	A	E	C	1	T 21.1, 20.1
Tree-hole tool use	1	1	1	A	A	A	A	A	A	A	C	1	T 21.1, 20.1
Straw tool	1	1	0	A	A	A	A	A	A	A	R	2,3	
Tooth cleaning (leaf)	2	0	1	H	A	A	H	?	C	A	A	1	T 21.1, 20.1
Tooth pick (stick)	2	0	0	?	A	A	A	?	?	P	R	1-3	T 21.2, 20.1
Artistic pillows	2	0	0	A	P	?	?	?	A	?	?	4	
Nest blanket	2	0	0	A	R	H	H	?	?	?	C	1	P 21.3.3
Nest lining	2	0	0	H/C	H/C	H/C	H/C	H/C	H/C	H/C	H/C	1	P 21.3.3
Nest pillow	2	0	0	H/C	H/C	H/C	H/C	H/C	H/C	H/C	H/C	1	P 21.3.3
Nest roof	2	0	0	A	?	H	C	C	C	C	C	1	T 20.1

Notes

Study sites include for Borneo: Gunung Palung (GP), Tanjung Putting (TP), Sabangau (SA) and Tuanan (TU), all *P. p. wurmbii*; and Kutai/Mentoko (KU) and Kinabatangan (KI), both *P. p. morio*; and for Sumatra: Suaq Balimbing (SB) and Ketambe (KE), both *P. abelii*. Prevalence of variants is referred to as: Absent (A), Present (P), Absent for ecological reasons (E), Habitual (H), Customary (C), or not known (?). Contexts are as in van Schaik, van Noordwijk et al. 2006: subsistence (1), physical comfort (2), and communication (3). 3)"Cultural" refers to the cultural status of the variant as described by Russon et al., 2009; Van Schaik et al., 2009. The classification of terrestrial versus exclusively arboreal tool variants, extractive-foraging (column name "EF"), and complex tool variants was based on the definitions described in paragraph 10.2.4 in the method section. Nest variants are printed in italic and could all be classified as complex whereas none of the other tool variants could be classified as complex. The "Ref" column mentions the most recent and complete references describing the particular tool variants and their presence data for the eight study populations (1= Wich et al., 2009; 2=Shumaker et al., 2011; 3= Meulman, unpublished data, 4= van Schaik et al., 2003). The "Source" column additionally indicates which Tables (T) or paragraphs (P) from Wich et al. (2009) were used to retrieve the data from. Tool variants for which short names were not reported before, or for which the definition or description has been modified, are: "Bee cover" (cover hat/body with leafy branches or leaves against stinging bees - not

swatting), “Branch hide” (combination of “hat hide humans” and “sneaky hat approach”), “Branch reach fruit” (use detached branch to reach incentive), “Branch fan” (fan themselves with branches for cooling), “Club” (tool for hitting a conspecifics with a piece of bark during agonistic interactions), “Aimed missile” (throwing or aimed dropping of branches, large fruits or other objects toward terrestrial predators (or humans), apparently to drive them away), “Stick push spine” (use a long stick to push a spiny Durian fruit into a crevice and thus protect hands), and “Hat cover” (use of leaves/leafy branches as head cover to protect against rain/strong sun/ etc. – different from ”Bee cover” in that usually fewer leaves or branches are used, which are moreover held less closely to the body). Only the variants “Branch dragging display” and “Stick as chisel (1-Nest)” were (sometimes) used in terrestrial contexts.

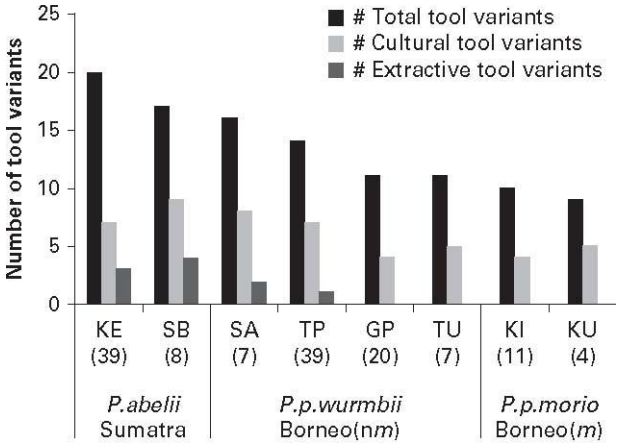

Figure 9.2 Overview of the number of tool variants, cultural tool variants and extractive-foraging tool variants per orangutan site. See the legend of Table 9.2 for study site abbreviations. Thirty-eight tool variants were recorded in total over all orangutan populations, of which 16 were cultural and seven were extractive-foraging tools. Both Sumatran populations (KE, SB) are on the higher end of the gradient with respect to the total number of tool variants, the number of cultural tool variants and the number of extractive-foraging tool variants. In parentheses is the approximate study duration in years for each research site.

Chimpanzees had significantly more complex (MWU = 20; $p = 0.036$), extractive-foraging (MWU = 6; $p = 0.001$) and terrestrial (MWU = 0; $p < 0.001$), but not cultural (MWU = 30; $p = 0.390$) tool variants per long-term study site compared with orangutans. The contexts in which tool variants were used also tended to differ between the two species ($\chi^2(2) = 5.58$; $p = 0.061$). Comparing each context separately, we found that chimpanzees had significantly more subsistence tool variants (MWU = 18.5; $p = 0.050$) than orangutans, significantly fewer physical comfort tool variants (MWU = 9; $p = 0.004$) and no substantial differences in the number of communication tool variants (MWU = 38; $p = 0.861$).

Variation in tool-repertoire composition

To establish the main components distinguishing tool repertoires across sites, and to gain some insight into the level of interdependency between outcome variables, we conducted a PCA. The Kaiser–Meyer–Olkin value of the combined set of variables indicated an adequate sampling (when communication variants were excluded – see discussion) for the analysis (KMO = 0.765), although not all KMO values for the individual outcome variables of the tool repertoire were above the acceptance limit of 0.5. Bartlett's test of sphericity ($\chi^2(21) = 177.196$; $p < 0.001$) indicated that correlations between the different outcome variables of the tool repertoire were sufficiently large for a PCA.

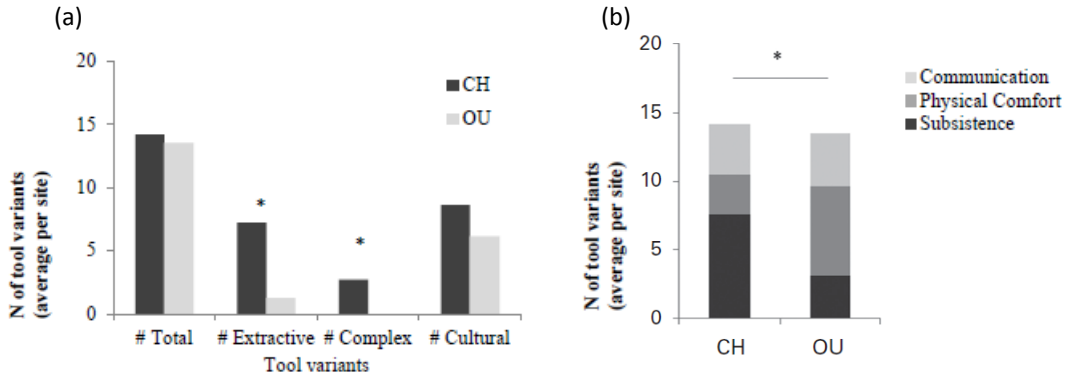

Figure 9.3 The tool repertoires of orangutans and chimpanzees compared. Average numbers for each subset of tool variants are reported to control for the number of study sites and the variation between them. In (a) the average number of tool variants in total, related to extractive foraging, ones that are potentially cultural according to the geographic method, or complex are reported for each of the two great ape species. (b) shows the average distribution of tool variants over the three contexts for the two great ape species. Chimpanzees had significantly more complex (MWU = 20; $p = 0.036$) and extractive-foraging (MWU = 6; $p = 0.001$), but not cultural (MWU = 30; $p = 0.390$) tool variants compared to orangutans. Also, the context in which tool variants were used did tend to differ between the two species ($\chi^2(2) = 5.58$; $p = 0.061$), with chimpanzees having significantly more subsistence tool variants (MWU = 18.5; $p = 0.050$) and significantly fewer physical-comfort tool variants (MWU = 9; $p = 0.004$) relative to orangutans. No substantial differences were found with regard to the number of communication tool variants (MWU = 38; $p = 0.861$).

Two components had eigenvalues larger than 1 (Kaiser's criterion) and in combination explained 92.9% of the variance (retaining two components was supported by the scree plot). The first component contained the total number of tool variants, the number of extractive foraging, cultural, complex, terrestrial and subsistence tool variants, whereas the second contained the total number of tool variants and physical-comfort tool variants (Table 9.3). In agreement with the predictions based on the refined model, the items that loaded highly on the

same components suggest that component 1 represents a general proficiency for the use of foraging tools, whereas component 2 reflects a propensity for using comfort tools.

Table 9.3 Results of a principal components analysis (PCA) of tool-repertoire outcome variables.

Tool repertoire (outcome variables)	**Component 1 (Foraging related)**		**Component 2 (Comfort related)**		**Component 3 (Communication related)**
Rotated factor loadings	−N−C	+N+C	−N−C	+N+C	+N+C
Extractive variants	0.987	0.854	−0.074	−0.411	−0.241
Subsistence variants	0.968	0.925	0.099	−0.191	0.213
Terrestrial variants	0.920	0.730	−0.269	−0.615	0.194
Cultural variants	0.893	0.900	0.357	0.115	0.339
Complex variants	0.885	0.952	0.066	−0.103	0.001
Total # variants	0.776	0.771	0.602	0.516	−0.122
Physical-comfort variants	−0.075	0.069	0.987	0.952	0.206
Nest element variants		−0.234		0.937	0.088
Communication variants		0.101		0.157	0.955
Eigenvalues	4.946	4.499	1.555	2.681	1.234
Percentage of variance	70.657	49.988	22.215	29.793	13.706

Notes

N = nest tool variants, C = communication tool variants, − = excluding, + = including. Positive factor loadings above 0.4 are printed in italic. Negative factor loadings below − 0.4 are printed in bold. N =18 study sites.

Testing the four factors of the model

Intelligence and the number of non-extractive and complex tool variants

The first prediction concerning the effect of intelligence was that the repertoire of non-extractive tool variants of Bornean *P. p. morio* is smaller than that of the other orangutans (Table 9.1). We compared the mean number of non-extractive tool variants for the two *P. p. morio* sites with that for all six other orangutan sites (Figure 9.4a). Although, as predicted, *P. p. morio* tended to have fewer non-extractive tool variants than the other orangutans, this difference was not significant (MWU = 0; p = 0.071). We also tested the between-species component of this prediction, namely that non-*morio* orangutans have equal-sized repertoires of non-extractive tool variants as chimpanzees (Figure 9.4b). However, the results show that non-*morio* orangutans have significantly more such tool variants per site than chimpanzees (MWU = 2; p = 0.001). Including *P. p. morio* in the analysis did not affect the results (MWU = 7; p = 0.002). We will examine this unexpected result in the discussion below.

The second prediction was that tool complexity of *P. p. morio* should be less than that of the other orangutans. Because the orangutan tool repertoire did not include any complex tool variants, it is not surprising that we did not detect any differences in tool complexity between *P. p. morio* and the other orangutans (MWU = 6; p = 1.000; Figure 9.4a). The

between-species comparison, however, showed that the various chimpanzee populations show a trend of having more complex tool variants than populations of non-*morio* orangutans (Figure 9.4b; MWU = 15; p = 0.093). When we included *P. p. morio* in the analysis, this result became significant (MWU = 20; p = 0.036). These findings either suggest that innovative ability (as indexed by brain size) does not affect complex tool use, or, more plausibly, reflect the combined effect of tolerant proximity and terrestriality (see below).

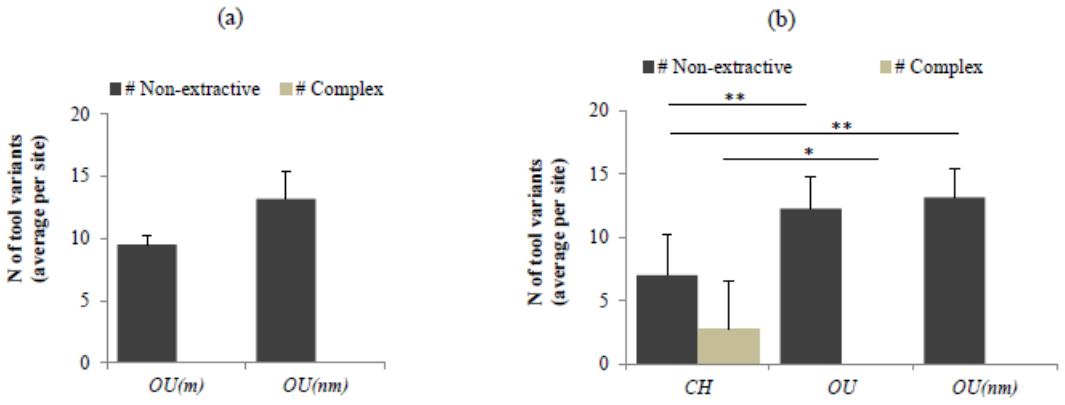

Figure 9.4 The role of intelligence on tool use reflected by the number of non-extractive tool variants and tool complexity. Figure (a) and (b) show the number of non-extractive tool variants as an indicator of innovative abilities, comparing (a) *P. p. morio* and non-*morio* orangutans (p = 0.071) and (b) chimpanzees and (non-*morio*) orangutans (p = 0.001) or orangutans (p = 0.002). The results indicate that *P. p. morio* shows a trend of having less non-extractive tool variants in the repertoire, and that orangutans have significantly more tool innovations in the non-extractive foraging context, compared to chimpanzees. Additionally, complex tool variants are compared between (a) *P. p. morio* and non-*morio* orangutans and (b) (non-*morio*) orangutans and chimpanzees. The mean number of complex tool variants did not differ significantly between the orangutan populations (p = 1.000), but a trend was shown when comparing chimpanzees to non-*morio* orangutans (p = 0.093), which reached significance when *P. p. morio* were included (p = 0.036); in favor of the chimpanzees).

Extractive foraging and the number of extractive-foraging tool variants

We predicted more extractive-foraging tool variants for Sumatran versus Bornean orangutans and similar numbers for non-*morio* orangutans and chimpanzees. The number of extractive-foraging tool variants in the local repertoire did not differ significantly (MWU = 0; p = 0.133) between non-*morio* Bornean orangutans and the Sumatrans (Figure 9.5a), probably due to the small sample size (n = 7). The Sumatra–Borneo difference did become significant when *P. p. morio* were included (MWU = 0; p = 0.036), suggesting that indeed the abundance of opportunities for extractive foraging may have some effect on the innovation of the relevant tools. However, orangutans showed significantly smaller local repertoires of extractive tool variants than chimpanzees (Figure 9.5b; MWU = 6; p = 0.007 for non-*morio*

orangutans; MWU = 6; p = 0.001 for when *P. p. morio* were included). This pattern can be explained by taking the terrestriality effect into account (see below).

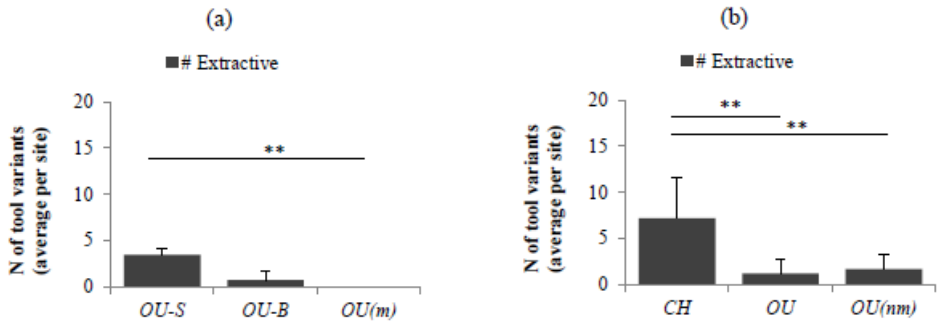

Figure 9.5 The role of extractive foraging on tool use. The number of extractive tool variants are compared between (a) Sumatran orangutans (*P. abelii*) and non-morio Bornean orangutans (*P. p. wurmbii*: p = 0.133, or p = 0.036 when *P. p. morio* were included), and (b) chimpanzees and non-*morio* orangutans (*P. abelii*, *P. p. wurmbii*; p = 0.007) or orangutans (including *P. p. morio*: p = 0.001), to evaluate the effect of extractive foraging tendencies. Thus, both Sumatran orangutans and chimpanzees have significantly more extractive-foraging tool variants in their repertoire than non-*morio* Bornean orangutans (*P. p. wurmbii*) and non-*morio* orangutans (*P. p. wurmbii* and *P. abelii*), respectively. However, this difference was only significant for the orangutan chimpanzee comparison, probably because of the small number of extractive tool variants within the orangutan tool repertoire (7 out of 38).

Social tolerance and the number of cultural tool variants

The number of cultural tool variants in the local repertoire may be smaller among non-*morio* Bornean orangutans than the Sumatrans (Figure 9.6a), but this difference was not significant (MWU = 1.5; p =0.400 when *P. p. morio* were excluded; p = 0.143 when they were included). Similarly, the non-*morio* orangutans did not seem to differ in the number of cultural tool variants from the more gregarious chimpanzees (Figure 9.6b; MWU = 26.5; p =0.728 when *P. p. morio* were excluded; MWU = 30; p = 0.390 when they were included). These results, therefore, do not support the contention that increasing opportunities for social learning positively affect the size of the cultural tool repertoire, or at least not to the extent we predicted based on the degree of gregariousness, but do make sense when the effect of terrestriality is included (see below).

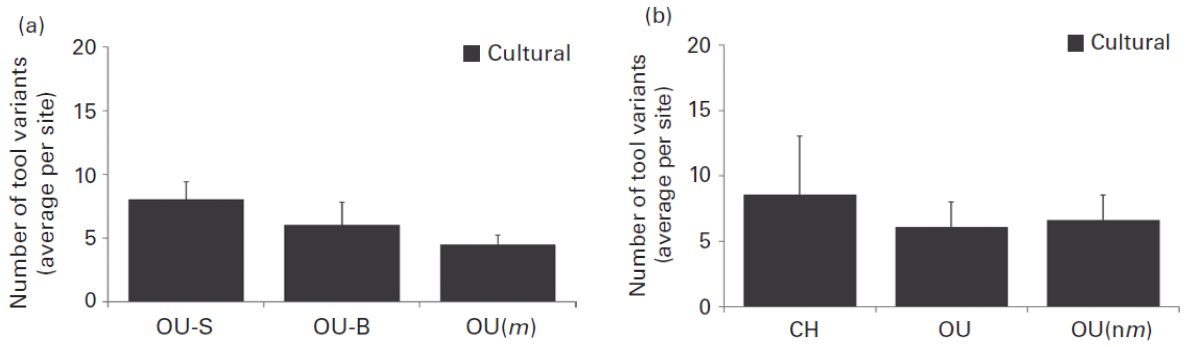

Figure 9.6 The role of social learning opportunities (based on the level of gregariousness), as reflected by the number of cultural tool variants. (a) The non-*morio* Bornean orangutans (*P. p. wurmbii*) have fewer cultural tool variants than the more gregarious Sumatran orangutans (*P. abelii*), although the difference was not significant (p = 0.400 when *P. p. morio* were excluded, or p = 0.143 when *P. p. morio* were included). (b) The more gregarious chimpanzees also tend to have more cultural variants compared to the less gregarious non-*morio* orangutans (p = 0.728) or orangutans (p = 0.390), but this difference was again not significant. Hence, social learning opportunities based solely on levels of gregariousness do not explain the variation in the number of tool variants in the cultural tool repertoire.

The effect of terrestriality

We predicted an effect of terrestriality, especially on the number of extractive (cultural) and complex (cultural) tool variants in favor of the more terrestrial chimpanzees in comparison to the arboreal orangutans (see Table 9.1). Above, we already found that chimpanzees indeed exceed orangutans in the number of extractive and complex tool variants. Likewise, chimpanzees surpassed orangutans in the number of extractive cultural (MWU= 6.5; p=0.009 when *P. p. morio* were excluded; MWU= 7.5; p=0.002when *P. p. morio* were included) and complex cultural (MWU= 3; p=0.002 when P. p. morio were excluded; MWU= 4; p<0.001 when *P. p. morio* were included) tool variants (Figure 9.7). Complex tool variants were, in addition, more often used terrestrially (MWU= 225.5; $p < 0.001$) (MWU = 225.5; $p < 0.001$) than non-complex tool variants. Including terrestriality as a factor thus explains why the effect of intelligence, extractive foraging tendencies and gregariousness per se, on the number of complex, extractive and cultural tool variants, is so limited when comparing orangutans and chimpanzees.

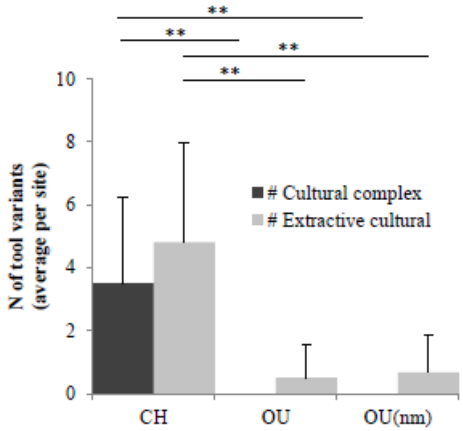

Figure 9.7 Effects of terrestriality on the cultural repertoire of (a) extractive-foraging tools and (b) complex tool variants; compared between non-morio orangutans (*P. abelii*, *P. p. wurmbii*)and chimpanzees. Relative to orangutans, chimpanzees have significantly more cultural tool variants for extractive foraging ($p = 0.009$ when *P. p. morio* were excluded; or $p = 0.001$ when *P. p. morio* were included) and complex cultural tool variants ($p = 0.002$ when *P. p. morio* were excluded, or $p = 0.001$ when included).

Discussion

Support for the refined model

When limiting the comparisons to orangutans only, the results support the original socioecological model (as well as the refined model, because orangutans are rarely terrestrial). First, the various outcome variables of the tool repertoire were always in favor of *P. abelii* and against *P. p. morio*, with *P. p. wurmbii* being intermediate (although mostly non-significant probably due to the small samples of tool variants in a specific category).The exception was tool complexity, because no orangutan population had complex tool variants. However, flexible and habitual use suggestive of social acquisition have only been reported for seed-extraction and tree-hole tool use, which are both exhibited only by (non-*morio*) Sumatran orangutans (van Schaik *et al.,* 1996, 2003b; van Schaik & Knott, 2001).

With regard to the results from the orangutan–chimpanzee comparisons, we found a significant bias toward extractive-foraging, complex, subsistence and terrestrial tool variants in favor of chimpanzees, whereas the bias was in favor of orangutans for the number of non-extractive and physical-comfort tool variants. These results did not support the original socioecological model and underlined the need for invoking a role of terrestriality. This, because the inclusion of terrestriality in the model, improves the fit between (1) opportunities for extractive foraging and the number of extractive tool variants; (2) brain size (as a predictor

for intelligence) and the number of complex tool variants; and (3) opportunities for social learning and the cultural tool repertoire. The PCA additionally illustrated a high correlation between terrestrial tool variants into the first component in which also cultural, complex, extractive-foraging and subsistence tool variants were clustered. In a previous study we furthermore found that, within chimpanzees, terrestrial extractive tool variants are more complex than arboreal tool variants (Meulman *et al.,* 2012). These results therefore suggest that terrestriality positively affects tool innovations, especially within the extractive foraging context; and, second, that, whereas opportunities for social learning are a necessary precondition for cultural tool variants, terrestriality is additionally needed to increase tool complexity.

Terrestriality versus complex arboreal tool use and nest building

We argue that the terrestriality effect is largely mediated by its effect on opportunities for social learning. A similar effect on tool complexity can therefore be expected for the arboreal honey extraction in chimpanzees when using pounding tools (Meulman *et al.,* 2012). Likewise, nest building can create a similar effect (again, see Meulman *et al.,* 2012). Strictly speaking, some variants of orangutan nest building should be regarded as tool use because they involve the detachment of vegetative material(s) from a fixed substrate (see Hansell & Ruxton, 2008 for a more detailed discussion). Interestingly, were we to consider nest-building variants tool use, we would indeed find complex tool use in wild orangutans.

One can also run the same argument in reverse. When a terrestrial context is not associated with enhanced opportunities for social learning, we should not expect to find complex tool use. For instance, male Bornean orangutans are fairly terrestrial but also almost exclusively solitary (apart from brief consortships with females, cf. Utami-Atmoko *et al.,* 2009). Indeed, we do not find any complex tool use in male Bornean orangutans.

The importance of species-specific innovation biases

The increased tool complexity in orangutans when including nest variants are in line with the differential challenges faced by orangutans and chimpanzees and the resulting innovation biases of orangutans toward comfort tools and of chimpanzees toward subsistence tools (see also van Schaik *et al.,* 2006). These innovation biases also explain the higher number of non-extractive tool variants for orangutans relative to chimpanzees that we could

not explain with the model (original or revised).

When we include the five nest elements as tool variants and redo the analyses we indeed find some interesting results. First, the difference between tool complexity in orangutans and chimpanzees, which was significant before, becomes non-significant (MWU = 25, p = 0.192 including *P. p. morio*; MWU = 21, p = 0.357 excluding *P. p. morio*). In addition, including the five nest elements changed the results of the PCA (KMO = 0.633; Bartlett's test of sphericity: $\chi^2(36) = 205.556l$, $p < 0.001$), so that extractive-foraging and terrestrial tool variants loaded strongly negatively on the physical-comfort component, which includes the nest elements (see Table 9.3). Moreover, inclusion of nest elements furthermore changed the percentages of variance explained by the foraging-(50% versus 70% when excluding nests) and comfort-related (30% versus 20% when excluding nests) components. Thus, although the foraging-related component still clearly outweighs the comfort-related component, the separation has become less strict. In conclusion, the lower tool complexity in wild orangutans may therefore largely be due to the innovation bias toward arboreal settings and the physical-comfort context.

The evolution of tool use in primates revisited

Based on the variation in orangutan and chimpanzee tool repertoires we can now extrapolate and see what these findings may mean for the evolution of tool use in primates (see Figure 9.8 for a schematic overview). The factors postulated by the original model (extractive foraging, innovative ability [i.e., intelligence] and opportunities for social learning [i.e., social tolerance]) remain relevant, but the effect of intelligence, extractive foraging and social tolerance is strongly affected by terrestriality, which therefore must be seen as an essential ingredient of the model.

Extractive foraging remains the basic precondition for tool innovations (Parker & Gibson, 1977; van Schaik *et al.,* 1999; Panger, 2007). Apes with extractive foraging have larger tool repertoires than the other apes (bonobos, gorillas) (McGrew *et al.,* 2007; Deblauwe & Janssens, 2008; Deblauwe, 2009; Lonsdorf *et al.,* 2009; Bentley-Condit & Smith, 2010), and among monkeys the only taxa with habitual tool use comprise extractive foragers that use tools mainly extractively (long-tailed macaques: Gumert *et al.,* 2009; capuchins: Visalberghi, 2009). Intelligence may compensate to some extent for the lack of an innovation bias toward the extractive-foraging context, but it has a limited effect on the occurrence of tool innovations in general, and even less on the occurrence of habitual tool use

or tools used for extractive foraging. This is reflected in the presence of non-extractive tool variants in all great apes (gorilla and bonobo tool use is almost exclusively non-habitual, non-extractive or even non-foraging related), whereas monkeys have virtually nothing in this regard (Ottoni & Izar, 2008; Gumert *et al.,* 2009; Bentley-Condit & Smith, 2010; Shumaker *et al.,* 2011).

Opportunities for social transmission determine subsequently whether tool innovations promoted by extractive foraging and intelligence can be maintained in the behavioral repertoire. Although social tolerance explains the presence of habitual tool variants (Whiten *et al.,* 2001; van Schaik *et al.,* 2003a; Leca *et al.,* 2007; Mannu & Ottoni, 2009), it is less important than terrestriality. Terrestriality is important because it facilitates an increased potential for complex innovations and skill acquisition through social learning. Terrestriality (and to a lesser extent also nest building) can therefore additionally explain the "orangutan tool paradox," and the occurrence of habitual and complex tool use in primates in general (for further discussion, see Meulman *et al.,* 2012).

Hominin evolution

The new version of the model (Figure 9.8) can also account for the flourishing of tool use into elaborate lithic technologies during hominin evolution. Since the emergence of the Oldowan, around 2.5 Mya, hominins were at least partially terrestrial, and used tools in terrestrial contexts (Plummer, 2004; Foley & Gamble, 2009). In addition, higher sociability (tolerant proximity), as implied by hunting of large game, allowed for more efficient information transfer. The rise of teaching following the adoption of alloparental care (cf. Burkart *et al.,* 2009) must have made transfer of technology to subsequent generations more efficient still. Thus, terrestriality, in combination with greater opportunities for social learning, afforded by greater sociability and teaching, goes far to explain the technological differences between great apes and humans (see also Meulman *et al.,* 2012).

Future directions

Although the new model can encompass the findings of this study, as well as the occurrence of true, habitual and complex tool use in general, the quality of the data could be improved to enable more quantitative analyses. First, more quantitative data on the frequency

of extractive foraging (perhaps even classifying whether tool innovations would be required or not) are important to more quantitatively assess the role of extractive foraging on the

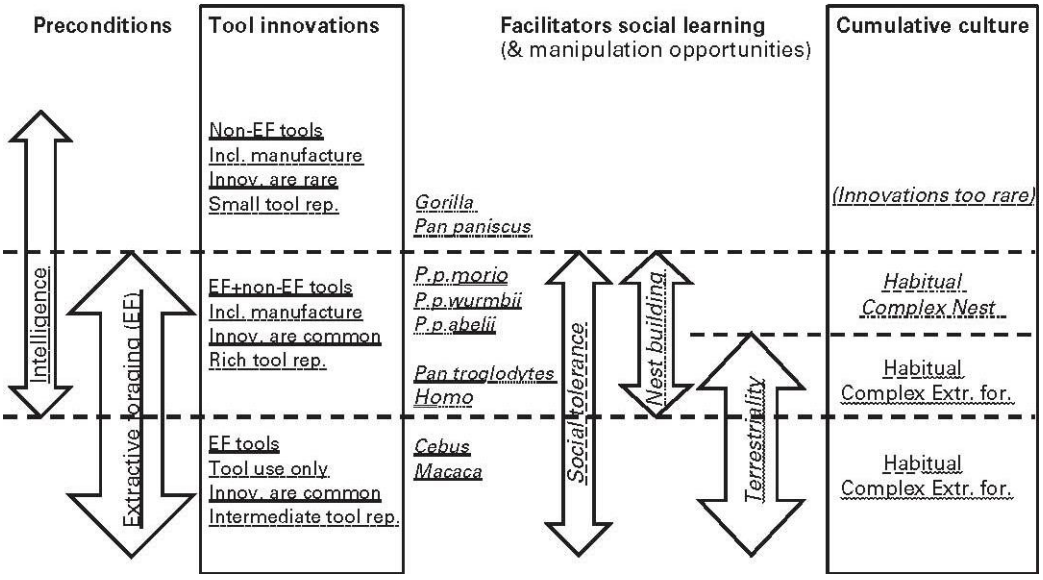

Figure 9.8 Diagram visualizing the five main evolutionary constraints acting on primate tool use. Predictor variables (or evolutionary constraints) are indicated by arrows. The gray rectangles describe the features of the tool repertoires based on these predictor variables. The width of the arrow is associated with its relative importance for the tool repertoire. The type of underlining indicates the link between the predictor variables and (1) the different features of the tool repertoire, as well as (2) how much they are represented in the different species. The dashed lines designate differences in predictor variables that affect the tool repertoires. Extractive foraging (indicated by EF or Extr. for.) seems to be the main driver for tool innovations (which become more common and diverse), although intelligence may compensate to some extent by its effect on innovative tendencies (also in the non-extractive-foraging context) and the complexity of these innovations (i.e., manufacture vs. use). Opportunities for social learning subsequently determine whether innovations may persist in the repertoire. Additionally, contexts such as terrestriality and nest building enable more complex manipulations and socially facilitated affordance learning, crucial for the manifestation of cumulative material cultures.

evolution of tool use. Second, it may be commendable to distinguish in the future between mere gregariousness and actual opportunities for social learning through observational learning, direct tool transfers and/or indirect tool transfers (or stimulus enhancement). Third, more specific data on variation in the level of terrestriality among populations and its consequences for social proximity and tool affordance learning would be crucial to confirm the importance of terrestriality for the evolution of cumulative technology and cultural intelligence. Especially data on social tolerance levels and socially facilitated skill acquisition in terrestrial contexts versus arboreal contexts would provide us with crucial empirical data in this regard. Likewise, more quantitative data are needed regarding the effect of terrestriality

on the occurrence of tool innovations and complex manipulations. Systematic comparisons of complex technology within the nest-building context (when socially learned) could similarly be very interesting and moreover provide more insight on the importance of innovation biases (e.g., chimpanzee versus orangutan nest building). Finally, more species and populations need to be included to confirm our conclusions for primates in general.

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CHAPTER 3

The role of terrestriality in promoting primate technology

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Abstract

''Complex technology'' has often been considered a hallmark of human evolution. However, recent findings show that wild monkeys are also capable of habitual tool use. Here we suggest that terrestriality may have been of crucial importance for the innovation, acquisition, and maintenance of ''complex'' technological skills in primates. Here we define complex technological skills as tool-use variants that include at least two tool elements (for example, hammer and anvil), flexibility in manufacture or use (that is, tool properties are adjusted to the task at hand), and that skills are acquired in part by social learning. Four lines of evidence provide support for the terrestriality effect. First, the only monkey populations exhibiting habitual tool use seem to be particularly terrestrial. Second, semi-terrestrial chimpanzees have more complex tool variants in their repertoire than does their arboreal Asian relative, the orangutan. Third, tool variants of chimpanzees used in a terrestrial setting tend to be more complex than those used exclusively in arboreal contexts. Fourth, the higher frequency in tool use among captive versus wild primates of the same species may be attributed in part to a terrestriality effect. We conclude that whereas extractive foraging, intelligence, and social tolerance are necessary for the emergence of habitual tool use, terrestriality seems to be crucial for acquiring and maintaining complex tool variants, particularly expressions of cumulative technology, within a population. Hence, comparative evidence among primates supports the hypothesis that the terrestriality premium may have been a major pacemaker of hominin technological evolution.

The main reason for the common statement that complex technology is the hallmark of human evolution is its unique degree of planning and motor coordination,[1] which is unrivaled within the animal kingdom.[2] However, findings on tool use among chimpanzees,[3] orangutans,[4] capuchin monkeys,[5,6] and, possibly, long-tailed macaques[7,8] show that habitual tool use in the wild is more widespread than previously thought. Moreover, these findings increasingly reveal ‘‘Oldowan-like’’ capacities in these primates, in terms of showing routine forms of tool use that involve the combination of multiple elements simultaneously or sequentially, transport, accidental flake production through percussive technology, and even (albeit rarely) the use of fracturing tools.[7,9–11]

Tool use is often considered to be cognitively more complex than other forms of object use because it involves relating multiple objects to one another.[12–15] In this paper, we are especially concerned with the evolution of ‘‘complex technology,’’ defined here as having three properties: flexibility, accumulation, and acquisition (at least in part) by social learning (see Box 1 for precise definitions).

First, flexibility in the selection, use, and/or transport of raw materials and in the dimensions of tools in relation to task requirements has been called ‘‘intelligent’’[16] and requires advanced innovative abilities,[17] extensive experience,[18] or both.

Second, in some cases, multiple objects or tools may be used simultaneously and complementarily to achieve a goal (combined tool use) or two or more tools may be used in a functionally integrated sequence for a single task (tool sets). Going one step beyond what, until now, has been observed for primates, Oldowan tool use may also have involved secondary tool use (the use of one tool to make another tool) or compound tools (when two or more elements of different types are combined into a single unit).[10] These four uses are examples of cumulative technology because they involve the addition of a new action to an existing one to create a new functional combination.[19] Such cumulative tool use is therefore thought to be cognitively demanding, if only in terms of working memory.[2,12]

Third, among primates the developmental acquisition of all complex skills has a major social-learning component. Indeed, wherever tool use is habitual in a primate population, it seems to be maintained by socially biased learning.[13,14,20–22] Moreover, many studies have shown that as tool-using skills become more complex, primates rely relatively more on social learning as opposed to exclusively relying on individual trial-and-error-learning.[13,14,23,24]

Box 1. Glossary

Technology—''the knowledgeable use of one or more objects as a means to achieve an end.''[27] This definition encompasses regular tool use and, for example, nest-building technologies.

Substrate use, borderline or proto-tool use—the manipulation of objects that remain part of the substrate they are attached to.[14,16]

Tool manufacture—''any structural modification of an object or an existing tool so that the object serves, or serves more effectively, as a tool.''[42]

Tool use—''manipulation of an object (the tool), not part of the actor's anatomical equipment and not attached to a substrate, to change the position, action, or condition of another object, either directly through the action of the tool on the object or of the object on the tool, or through action at a distance as in aimed throwing.''[16] (See Box 2 for discussion of the choice of this definition.) Objects used in play or potential play (that is, seen once by a younger individual so that playing purposes could not be excluded) were not included in this study, with the exception of ''play start'' and ''self-tickle,'' which have consistent actions and results.[3] Orangutan nest elements (nest pillow, blanket, lining, roof) were excluded from analyses because the inclusion of such elements as tools (although, according to the definition they are) is still controversial (but see discussion). As in Whiten and coworkers[85] and Sanz and Morgan,[3] the criteria for lumping or splitting tool variants was based on whether the action patterns appeared to be similar or not.

Complex technology—a technological variant that is acquired at least in part by social learning and for which manufacture or use is both flexible and accumulated.

Flexible tool use—tool use in which tool features are adjusted or modified according to the specific requirements of the task at hand, depending on the need or in order to increase efficiency or functionality (modified from van Schaik[39]).

Accumulated (cumulative) tool use—the addition of a new action to an existing one to create a new functional combination or sequence to reach an overall goal.[2,19] We considered tool use to be accumulated only when it involved the functional integration of multiple elements; that is, for primates the use of tool sets or combined tool use.

Combined or composite tool use—the simultaneous and complementary use of two tools to achieve a goal, as a hammer and anvil in nut cracking.[10]

Sequential tool use—the use of multiple tools in a sequence. Two types can be distinguished: tool-set use and secondary tool use.[54]

Tool set use—''the obligate sequence of two or more tools used to achieve a single goal.''[10]

Secondary tool use—the use of one tool to make another; for example, stone knapping.[54]

Compound tools—tools made of two or more elements of different types that are combined into a single unit. For instance, spears, knives, and scrapers may consist of a handle or shaft, a stone insert, and a binding material.[10]

Social tolerance—can be defined in several ways that, to a large extent, correlate. Thus, species are considered socially tolerant when they show greater proximity during foraging, higher rates of food transfers, and low rates of aggression or more symmetric aggression.20,22

Social learning—this encompasses not only observational learning, but also any kind of additional individual learning that is triggered or influenced by other group members or conspecifics (modified from Fragaszy and Perry[14]). The latter is also referred to as socially biased or mediated (individual) learning.

Affordance learning—a ''process whereby an observer detects stimulus consequences, such as dynamic properties and temporal-spatial causal relations of objects by watching the object movements.''[83]

Extractive foraging—''the act of locating and/or processing embedded foods such as underground roots and insects or hard-shelled nuts and fruits.''[84]

Semi-terrestrial—spending time on the ground as well as in trees.

Habitual tool use—tool-use variants that have been seen repeatedly in several individuals and are consistent with some degree of social transmission (sensu McGrew and Marchant[43]).

Cultural intelligence—intelligence acquired through social learning (sensu Whiten and van Schaik[49]).

Zone of latent solutions— the species-specific behavioral predispositions to innovate in particular contexts (sensu Tennie et al.[5]).

Box 2: Defining Tool Use

In recent years, we have seen a variety of updated definitions of tool use. Shumaker, Walkup, and Beck[42] discussed these in detail and subsequently came up with the most recent definition, based on the original definition from Beck[15] (words in italics represent the modifications): ‘‘Tool use is the external employment of an unattached or manipulable attached environmental object to alter more efficiently the form, position, or condition of another object, another organism, or the user itself, when the user holds and directly manipulates the tool during or prior to use and is responsible for the proper and effective orientation of the tool.’’[42:5]

Although their inclusion of ‘‘manipulable attached’’ was meant to reduce the perhaps somewhat artificial distinction between tool use and borderline, substrate, or proto-tool use, in our perspective it has a disadvantage when dealing with hominin technology. In examining the role of terrestriality in promoting primate technology, the fact that objects are ‘‘not attached to a substrate’’ is very important, because such detached objects are generally more salient, can be more easily modified, and can be more flexibly incorporated into a tool combination or sequence. Therefore, for the current purpose, the definition formulated by Parker and Gibson[16] is more appropriate.

Another concern arises with Shumaker, Walkup, and Beck’s (as well as Beck’s original) incorporation of the word ‘‘efficiently.’’ In our opinion, efficiency is at least sometimes difficult to measure; insistence on it would exclude unsuccessful tool use (for example, by immatures) from being considered tool use, which is problematic, as Shumaker Walkup, and Beck rightly point out. In fact, even for adults or proficient tool users, the use of tools does not always need to be more efficient: it may also increase comfort, have no additional value, or even be less efficient. For instance, if one first uses a fork and knife to handle food and subsequently, but less efficiently, uses chopsticks, should the use of fork and knife be considered tool use whereas the use of chopsticks is not? And are they both more efficient than eating with one’s hands?

Shumaker, Walkup, and Beck[42] found the definition of tool use we used here, which was originally formulated by Parker and Gibson,[16] to be problematic because of the inclusion of ‘‘or object on the tool.’’ They argued that this inclusion makes the distinction between true tool use and proto-tool use less clear. Although Parker and Gibson do not specifically go into this, we believe that there is only one possible interpretation of this sub-phrase, namely, that the tool may be manipulated beforehand to become considered a tool. The position, action, or condition of the object can subsequently be changed by the action ‘‘of the object on the tool,’’ as when one hits a nut (object) on a manipulated anvil (tool). Shumaker, Walkup, and Beck seem to include a similar addition with the ‘‘when the user holds and directly manipulates the tool during or prior to use....’’

We thus prefer to adopt the definition from Parker and Gibson[16] because it is more relevant and applicable to discussions of human evolution.

We should emphasize that use of the term ‘‘social learning’’ here does not imply the presence of dedicated social-learning modules, but merely that of social inputs into the individual learning process (also referred to as socially biased learning), which may vary from local or stimulus enhancement to affordance learning via the implements of others, and to

observational learning of actions or goals as in imitation or emulation.[13]

A major unsolved question is what drove the evolution of the human capacity for complex technology. We propose that terrestriality has strongly facilitated the technological sophistication observed in some extant primates by affecting not only the probability of tool innovation, but also the probability that such innovations will be socially transmitted and hence maintained within a population. This may have been of crucial importance for the evolution of cumulative hominin technology.

Terrestriality as a facilitating condition

Previous studies and reports on tool use in primates have often emphasized the role of extractive foraging, dexterous manipulative abilities, and intelligence.[14,16,21] In addition, Coussi-Korbel and Fragaszy[25] and van Schaik, Deaner, and Merrill[20] stressed the special role of social tolerance for the occurrence of social learning in the spread and maintenance of tool-using skills within a population.[20,25] We propose that terrestriality affects these three major components of the technology process: innovation, accumulation, and social learning.

Innovation may be facilitated by terrestriality. As emphasized by various authors, it affects the availability of food and of raw materials to be used as tools[6,26,27] because terrestrial contexts present a wider range of possible substrates and tool materials, such as stones and grass stems in addition to twigs and leaves.[26,27] Also, in terrestrial settings, in contrast to arboreal contexts, hands are often no longer needed for positional support, which may enhance innovation by allowing more actions on objects, as well as the use of complex actions that require the coordinated involvement of both hands[13,28,29] or hand specialization.[30–32]

The accumulation of complexity may also be facilitated by terrestriality because tools stay at the place where they are used whereas, in arboreal settings, tools tend to disappear after being dropped. The continuous availability of tools at a terrestrial tool site, such as the hammers and anvils used in cracking nuts[33–35] or the puncturing implements found at a subterranean termite nest,[36] should enhance opportunities for the accumulation of techniques. Thus, the presence of previously made tools in terrestrial but not arboreal settings may enhance the invention or use of tool sets, which requires more elements that need to be innovated to obtain the single goal (sequential tool use) and increase the likelihood that users

combine tools (composite tool use), add further elements to the tool (compound tool use), or use tools to manufacture additional tools to improve their effectiveness (secondary tool use).

Social learning is also likely to be enhanced by terrestriality because the arboreal constraints imposed by the architecture of the canopy are missing. In terrestrial settings, learners can often come in closer proximity to experts[37] and their view is less likely to be blocked by vegetation. In addition, the learner usually has access to the tools after their use by these experts because tools mostly stay at the site where they are used. This provides opportunities for extensive affordance learning, unlike in arboreal contexts where tools are rarely conserved. Indeed, with regard to the latter, Liu and colleagues[38] found that wild bearded capuchins were significantly more likely to use the pit where the preceding individual last struck than to use other pits.[38] In particular, this effect of terrestriality on affordance learning may promote opportunities for horizontal or oblique social transmission in addition to vertical transmission. This increases the likelihood for innovations to spread throughout a population beyond the mother-infant context, and hence to become habitual. Such extra opportunities for social transmission are even more important for preventing the disappearance of complex innovation from a population's behavioral repertoire because repeated individual innovation is here even less likely.

As a result of these proposed terrestriality effects on innovation, accumulation, and social learning, terrestriality may promote complexity of technological skills because of the increased potential for affordance learning in this context, especially in the case of nonperishable materials.[19] In other words, ceteris paribus, given a species' intrinsic predispositions for tool innovation and social learning, a terrestrial population is more likely to discover and exhibit habitual tool use that is of higher complexity than would an exclusively arboreal population of the same species.

In this paper, we evaluate predictions that follow from the terrestriality effect on the occurrence of complex tool use in primates. Because complex innovations are unlikely to occur at once, but commonly build on simpler initial innovations, some kind of initial routine tool-use tendency needs to be present to function as a foundation for more complex forms of habitual tool use to develop. Only orangutans, chimpanzees, capuchins, and probably long-tailed macaques exhibit flexible and habitual tool use in the wild, probably as a result of their tendencies for dexterous extractive foraging and social tolerance in these contexts.[20] We will specifically examine these species to test the terrestriality effect on tool complexity. Most terrestrial primates do not exhibit the preconditions for habitual tool use. Some, such as

gorillas and bonobos, lack a strong penchant for extractive foraging. Others lack the level of social tolerance that allows social transmission of such foraging techniques; for example, baboons are too despotic, as are most macaque species.[20] Therefore, a terrestrial lifestyle per se is unlikely to enhance the complexity of tool repertoires.

We propose that in species having a predisposition for tool use (that is, dexterous extractive foragers), the innovation, accumulation, and maintenance of such use can be promoted by terrestriality. In particular, we develop four predictions. We predict that in monkeys the extra opportunities for innovation and affordance learning provided by terrestriality allow for the spread of ''incidental tool use'' beyond individual innovations. Hence, only in those populations that combine dexterous extractive foraging strategies with both social tolerance and terrestriality do we expect to find habitual and complex tool use (prediction 1). For the tool-using great apes that are dexterous extractive foragers (orangutans and chimpanzees), we predict that terrestriality mainly affects the complexity of tool use rather than its habitual presence in the population per se. We therefore predict that the semi-terrestrial chimpanzees exhibit more complex tool-techniques than do the almost exclusively arboreal orangutans (prediction 2). Within chimpanzees, we predict that tools used in terrestrial contexts are more complex than tools used exclusively in arboreal contexts (prediction 3). We also predict that the ''tool paradox,'' according to which captive animals tend to show far greater tool-using skills than do their wild conspecifics,[39] is strongest in species that, in the wild, are usually arboreal (prediction 4).

We expect a terrestriality effect on tool use among captive primates for the following reasons. First, terrestrial settings, which are predominant in captivity, may facilitate innovation because both hands can be used in object manipulation. Second, these innovations may be of higher complexity because tools remain available in the enclosure after use and are often salient. Third, in captivity social learning is enhanced by exposure to the implements used by others and by the closer proximity of tolerant individuals. Obviously, however, we should not forget that such a captivity effect on tool use may also depend in part on other factors, such as the increased innovation rate resulting from the radically different attitude toward novelty among captive or rehabilitant animals, the amount of free time they have, and enculturation effects.[13,40,41]

Testing the terrestriality effect

Monkeys, Tool Use, and Terrestriality

Reports about monkeys' object use indicate that most populations overwhelmingly show only substrate use or true tool use that is of low complexity and/or incidental in its occurrence.[42] Habitual tool use in monkeys (*sensu* McGrew and Marchant[43]) has been demonstrated only among capuchin monkeys that live in savanna-like habitats[21] and, probably, long-tailed macaques inhabiting the coastal region of the Piak Nam Yai Islands and the islands of the Mergui Archipelago in the Andaman Sea. (In the latter case, habitual use of tools was inferred without individual recognition of the monkeys.[7]) Some of these populations even have tool kits containing multiple different tool types.[5,7] Interestingly, all these monkey populations seem to be more terrestrial than are other populations within their taxon.[6,26,44–47]

These findings support the conclusion that only monkey populations that are dexterous extractive foragers, socially tolerant, and terrestrial exhibit habitual tool use, whereas such potential traditions are absent in other, more arboreal, wild monkey populations. However, two issues remain to be resolved before this conclusion can be fully accepted. First, an apparent exception may be arboreal termite fishing by tufted blond capuchins.[48] However, this arboreal tool use has been observed only eight times during a total of 72 days for three of the six individuals in the group (all adult males), whereas all individuals were foraging for termites on a daily basis. Thus, it is as yet unclear whether this tool use is habitual according to the definition of McGrew and Marchant.[43] Moreover, the forest fragment these capuchins inhabit is surrounded by a monoculture of sugar cane, suggesting that, at least in part, they have semi-terrestrial life styles. Currently, however, observational data from these capuchins in the more terrestrial habitat is lacking. Hence, the reported absence of evidence of terrestrial tool use still needs to be verified. Second, our hypothesis requires high social tolerance among the long-tailed macaques of the Andaman Islands but, at present, no data are available.

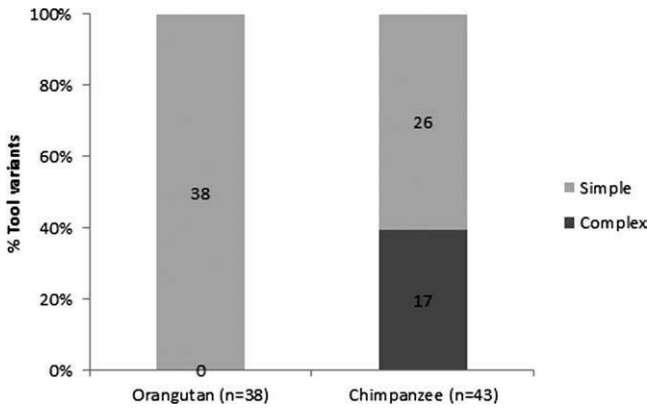

Figure 1 Tool complexity of orangutan and chimpanzee tool repertoires. Within a tool repertoire of 38 and 43 tool variants for orangutans and chimpanzees, respectively, chimpanzees have significantly more complex tool variants (that is, flexible, accumulated, and acquired at least in part by social learning) in their repertoire than do orangutans (Pearson $X^2(1)$ ¼ 19.014; $p < 0.001$). Descriptions of orangutan tool variants are reported in Meulman and van Schaik.[4] For chimpanzee tool variants, see Table 1.[3,4]

The Arboreal Orangutan Versus the Semi-Terrestrial Chimpanzee

Orangutans and chimpanzees are both intelligent and extractive foragers.[4] Differences in tool repertoire have therefore mainly been ascribed to differences in social tolerance.[22] Indeed, a recent compilation of orangutan tool repertoires from eight wild populations[4] indicated that repertoire size and the number of cultural variants within this repertoire did differ within the species, as reported by Whiten and van Schaik.[49] However, chimpanzees have significantly more complex tool variants (that is, flexible, cumulative, and acquired at least in part by social learning) in their tool repertoire than do orangutans (Pearson $X^2(1) = 19.014$; $p < 0.001$; Fig. 1). Extractive foraging tendencies, intelligence, and social tolerance could explain only part of the variation observed between these apes.[4] The terrestriality effect, however, seems to provide a more complete explanation for the differences in tool complexity between these two great apes.

Terrestriality and Tool Complexity Among Chimpanzees

If terrestriality induces greater technological complexity, one would expect that chimpanzee tools used in terrestrial contexts would be more complex than tools used exclusively in arboreal contexts. Indeed, this is the case. As previously defined, complex tool use by chimpanzees has so far been found exclusively in terrestrial contexts: nut-cracking, termite-fishing, ant-dipping, and honey-extraction, with the partial exception of arboreal honey extraction (Table 1).[12,50–54] Because extractive foraging tools, which are used to extract edible

Table 1 Chimpanzee Tool Variants, Context, Complexity, and Use for Extractive Foraging

Tool variant[3,85,86]	Exclusively arboreal	Complexity
Aimed throw	No	Simple
Algae scoop	No[87]	Simple
Ant dip, single	No[52]	Complex[52]
Ant dip, wipe	No[52]	Complex[52]
Ant fish	No*	Simple
Ant nest perforation[52]	No	Complex
Anvil prop	No	Complex
Bee probe	No[88]	Complex[53]
Branch drag	No[89]	Simple
Branch hook	Yes[90]	Simple
Club	No	Simple
Comb	No	Simple
Container	Yes[91]	Simple
Dig	No[90]	Complex
Expel/stir	No[92]	Simple
Fluid dip	No[88]	Complex
Fly whisk	Yes[93]	Simple
Insect pound	Yes[90]	Simple
Investigatory probe	No[94]	Complex
Leaf brush	No[91]	Simple
Leaf clip	No[95]	Simple
Leaf dab	No[42]	Simple
Leaf mop	Yes[91,96]	Simple
Leaf napkin	No	Simple
Leaf sponge	No	Complex[97]
Leaf wipe	No[91]	Simple
Lever open	No[91]	Complex
Marrow pick	No**	Simple
Nasal probe	No[98]	Simple
Nut hammer	No	Complex[88]
Nut-extraction tool	No[88]	Complex[88]
Perforate termite nest	No[36]	Complex
Pestle pound	Yes[99]	Simple
Play start	No	Simple
Pound beehive	Yes[51,53]	Complex
Puncture termite nest	No[36]	Complex
Rain cover	Yes	Simple
Resin pound	Yes[90]	Simple
Seat stick	Yes[100]	Simple
Seat vegetation	No	Simple
Self-tickle	No[91]	Simple
Sponge push-pull	Yes[42,97]	Complex[97]
Termite fish	No	Complex

Notes

Tool variants were listed according to Sanz and Morgan[3] and categorized as respectively complex (1) or not (0), used for extractive foraging (1) or not (0), and used exclusively in arboreal contexts (1) or not (0), using the definitions reported in Box 1. This classification was based on the definitions and references provided by Sanz and Morgan[3]; Whiten, Goodall, and McGrew[85]; and Nishida and colleagues.[86] Numbers in superscript refer to references used in addition to these. *Rob O'Malley, personal communication. **Paco Bertolani, personal communication.

food items from the matrix they are embedded in, have more potential for complexity than do, for example, tools used for grooming or social interactions, they should be especially subject to the terrestriality effect. Indeed, extractive terrestrial tools in chimpanzees show a trend (despite the very small sample size) toward being more complex than tools used exclusively

in arboreal contexts, (Fisher's exact test, $X^2(1) = 3.811$; $p = 0.089$; Fig. 2). This increase in tool complexity may be due to terrestriality-induced opportunities for social learning, as well as enhanced opportunities for hand use and hand specialization, given the constraints on hand use in the trees. Indeed, with regard to the latter, handedness has been observed for terrestrial but not arboreal tool use.[30,31] Terrestriality thus seems to promote the acquisition and maintenance of complex tool-using skills in chimpanzees (that is, combined or sequential tool use for extractive foraging).

The ''Tool Paradox''

The prediction was that the terrestriality effect on technology would be strongest in species that are normally arboreal. It is difficult to quantify this, but the effect of captivity on technological skills was noted especially for orangutans, capuchins, and macaques,[15] all of which are generally arboreal taxa. Among orangutans, the ''tool paradox''[39] has been discussed for years: Captive orangutans are accomplished tool users[15,55–57] whereas, in the wild, flexible tool use is limited to only a few populations.[58,59] Moreover, complex tool use has been observed various times in captivity,[42] but has never been observed in the wild (excluding tool use by combining the same elements without any modification or manufacturing steps in between, such as hand glove).[4] A similar contrast was noted for capuchins, at least until the findings on the semi-terrestrial capuchins were reported.[15,42,43,60,61] Arguably, the same may be true for macaque tool use.[7,15,42,49] For semi-terrestrial chimpanzees, however, no such contrast is found.[18,43] Hence, the captivity effect seems to be particularly prominent for technological skills in arboreal species, for which terrestriality seems to provide an apt explanation. However, we are aware that other factors could also contribute to the discrepancies between captive and wild technological skills.[13,40,41]

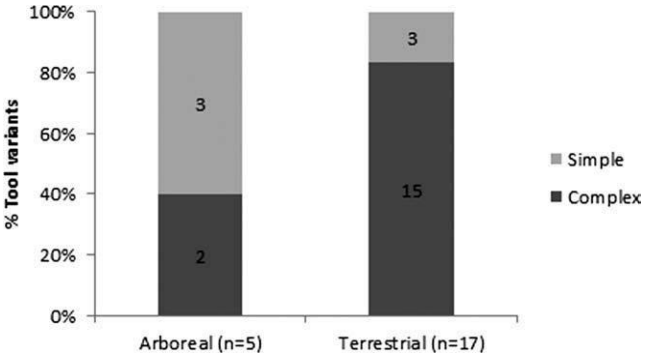

Figure 2 The distribution of complex extractive foraging tool variants according to context in chimpanzees. Of a repertoire of 43 tool variants,[3] we defined 23 as extractive foraging tools. Five of these were used exclusively in arboreal contexts and 18 in terrestrial and arboreal contexts. Terrestrial tools are more complex than tools used exclusively in arboreal contexts (Fisher's exact test, $X^2(1) = 3.811$; $p = 0.089$). For more detailed information, see Table 1.

Discussion

Various scientists have hinted at a positive effect of terrestriality on the likelihood of tool innovation;[26,27,32,62] but see Boesch-Achermann and Boesch[63] for a different view. However, the present study is the first, to our knowledge, to propose that terrestriality promotes not only the acquisition, but also the transmission and complexity of skills by affecting both the probability of innovation and socially biased learning. This way, terrestriality may promote the skills an individual is able to acquire over its lifetime (which is indicative of its cultural intelligence) as well as the accumulation of complex innovations that may be socially transmitted; that is, cumulative technology. The comparisons discussed earlier show that there is, indeed, evidence of an effect of terrestriality on the complexity of primate technology. We will discuss additional, more indirect evidence and point to future studies that can provide definitive tests of our assertion. We will end by discussing the implications for understanding technological evolution in hominins.

Further Tests of the Terrestriality Effect

An apparent anomaly is the occurrence of complex arboreal tool use by chimpanzees in the form of the use of tool sets in honey extraction. We argue here that this is nonetheless consistent with the terrestriality effect. First, it appears that this complex arboreal technique is actually derived from other complex forms of terrestrial tool use. Because many populations are still understudied, any conclusions are still preliminary. Nonetheless, we know that all

chimpanzee populations that use tool sets in arboreal honey extraction also use tool sets in terrestrial activities: honey extraction, termite fishing, and ant dipping.[36,51–53] This is consistent with terrestrial origins for complex arboreal techniques. This interpretation is supported by Yamamoto's[64] observation of an individual applying and subsequently modifying terrestrial ant-dipping techniques to arboreal contexts, eventually inventing a new arboreal ant-fishing technique.[64]

Second, opportunities for learning tool affordances through tools and through activities performed by others, which are important in terrestrial tool use, also seem likely in arboreal honey extraction. Thus, chimpanzees use very conspicuous tool techniques, including distinctive pounding, which can be seen and heard by others from a great distance. Moreover, because the tools used are numerous and large, they are prominent when placed in the canopy or dropped at the tool site.[51,53] This contrasts with the much less complex and conspicuous arboreal ant fishing, even though tool sets have been observed for terrestrial ant dipping.[52] Therefore, opportunities are abundant for the maintenance of such a complex skill within the population through social learning, which resembles a terrestriality effect.

The terrestriality effect on tool complexity may also apply to other technological contexts, such as nest building. Here again the exception seems to prove the rule because many elements prominent in the terrestrial context are found in this arboreal activity. Nests decay only slowly, and thus provide more opportunities for stimulus enhancement by reuse or sharing than do other arboreal technological contexts. Moreover, as in chimpanzee arboreal honey extraction, the branch breaking and vocalizations that accompany nest building may attract the attention of other group members or associates and therefore offer opportunities for local enhancement. In addition, the highest rates of selective visual attention by infants are observed in this context. Because animals are often comfortably seated during these activities, and therefore have both hands free, hand specialization is also made possible. Indeed, this is exactly the context in which the arboreal orangutans show their most complex technologies, including flexible and combined use of different elements, such as a nest pillow, nest blanket, nest roof, and nest lining, in a manner similar to the sequential or combined tool use by chimpanzees. Nest building usually is not regarded as tool use,[15,42,65] even though, strictly speaking, it often fits the definitions (see Hansell and Ruxton[65] for a discussion of this topic). Nonetheless, it seems that, just like chimpanzees' use of complex tools for arboreal honey extraction, orangutan nest building provides an example of complexity in arboreal technology

induced by a terrestriality-like effect in terms of opportunities for social learning.

Although comparative evidence among primates suggests enhanced tool complexity in terrestrial contexts, populations, and species, targeted studies are still needed to confirm the direct link between terrestriality and socially facilitated tool affordance learning as the main proximate mechanism underlying the effect of terrestriality on the occurrence of habitual complex tool use. We predict that among chimpanzee populations, variation in the degree of terrestriality and associated tool-use opportunities across populations is correlated with variation in the complexity of the tool kit.

We also predict that immature chimpanzees and capuchins acquire terrestrially used skills at a younger age than that they acquire arboreal skills, provided we control for complexity. To our knowledge, no study has directly examined the developmental acquisition of tool-using skills in terrestrial versus arboreal contexts. We also predict that immatures spend more time practicing with tools previously used by experts when on the ground rather than in trees. Indeed, the findings reported by Carvalho and coworkers[35] on chimpanzee tool recycling (re-use) do suggest such correlations, as do reports of capuchins' repeated use of the same anvil, the same anvil pits, and/or the same hammer stones.[33,38] In line with the latter point, we also predict that for tasks in which tools of others are frequently encountered, the techniques that are applied become more complex relative to tasks where such tools are not readily available for affordance learning. The previously described complex technology for arboreal honey extraction and nest building are in line with such an effect. Moreover, preliminary data suggest that the terrestriality effect may even induce higher levels of social tolerance, especially toward infants.[37]

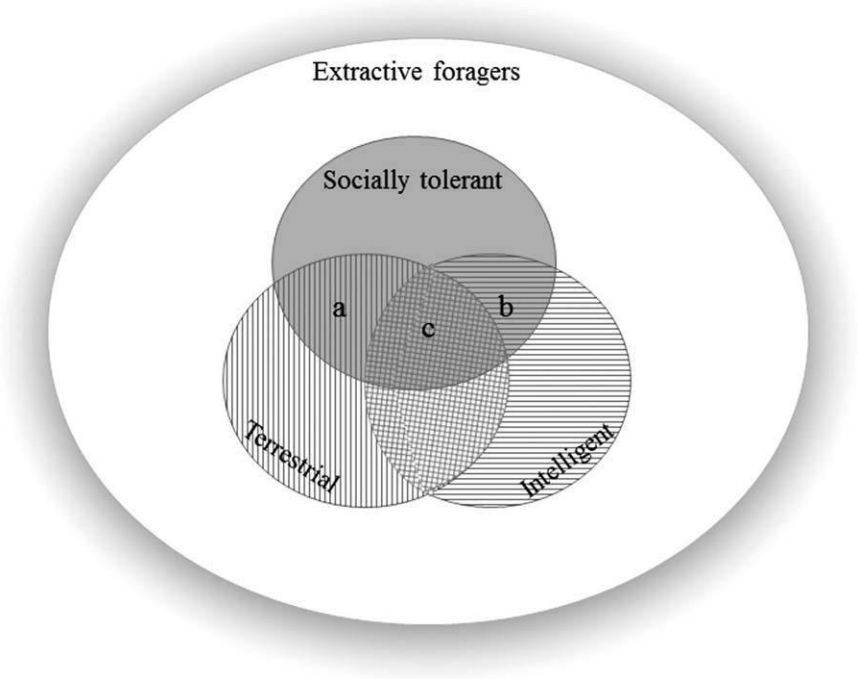

Figure 3 Diagram illustrating the selective pressures underlying the evolution of tool use in primates. A certain level of dexterous extractive foraging is an essential precondition for the occurrence of tool innovations.[20] These innovations may become habitual, through social transmission, and more complex, in conditions of high social tolerance. Where such species or populations are additionally (a) terrestrial or (b) more intrinsically innovative or intelligent, more complex tool use is expected. The most complex tool use is expected where both terrestriality and intelligence act together, in addition to dexterous extractive foraging and social tolerance (c).

In conclusion, the available evidence supports the idea that terrestriality may partly compensate for constraints on innovation and social learning abilities. First, terrestriality may enable socially tolerant monkeys that are also adept dexterous extractive foragers to exhibit more habitual and complex tool use than do members of the same species in an exclusively arboreal setting. Second, terrestriality may explain why semi-terrestrial chimpanzees, as well as captive and rehabilitant orangutans, outperform wild orangutans in their tool complexity, despite having a very similar extractive-foraging niche and intrinsic cognitive potential. This new model is illustrated in Figure 3.

How Terrestriality May have Shaped Human Evolution

Assuming that future studies will uphold the terrestriality effect, we now turn to its implications with regard to our understanding of hominin evolution. Most populations of the four habitual tool-using primate species (chimpanzees, orangutans, capuchins and, possibly, long-tailed macaques) spend a considerable amount of their time in trees. However, some populations have become semi-terrestrial through lack of a continuous canopy, living in

habitats with reduced predation risk, or the presence of food resources on the ground.[5,8,21,72] We should emphasize that although such ecological changes promoted semi-terrestrial lifestyles in many species,[73] they do not necessarily promote the occurrence of tool use or extractive foraging per se. This is especially true for species in which extractive foraging and tool innovations are not in the zone of latent solutions (*sensu* Tennie, Call, and Tomasello[75]), such as gorillas, bonobos, and numerous catarrhines.[68,73–75] Indeed, capuchins currently inhabiting savanna-like habitats engage in all kinds of activities on the ground, not just extractive foraging or tool use.[6,76] Hence, initial tool-use tendencies fostered by dexterous extractive manipulative skills and social tolerance must be present to allow for the suggested terrestriality effect on tool innovation, diffusion, and complexity.

The flourishing of technology among hominins is consistent with the terrestriality effect. First of all, evidence suggests that the climatic changes during the Late Pliocene (around 3 Ma) forced catarrhines in general, and early hominins in particular, to become more terrestrial.[73,77] Moreover, by the emergence of the Oldowan, around 2.5 Ma, our ancestors were at least partially terrestrial, as strongly indicated by fossil evidence.[77,78] Hence, their tool use has probably also been subject to the terrestriality effect, especially when such tool use involved stones, which are available only in terrestrial settings, and tools to scavenge or hunt terrestrial animals.[77,78]

Although new findings of fossils and tools over the last two decades has provided some crucial insights on hominin evolution, this evidence still leaves a lot of room for uncertainty as to the function or adaptive value (for example, bipedalism and tool use) and process of morphological changes. This uncertainty can be reduced through comparison with observational, archeological, and morphological data from extant primates. Although such research is still in its infancy, preliminary studies suggest that correlational studies on sex-, age-, and population-related variation in morphology and behavior, such as locomotion patterns and manipulative skills, can yield important insights. For example, the different hand morphology found for western versus central chimpanzees might account for variation in nut-cracking behavior.[29] Similarly, archeological comparisons of stone tools from chimpanzees and early hominins suggest instructive similarities and differences.[79] Finally, variation in morphological features with known function in other primates can be linked to certain foraging strategies and locomotion patterns, as well as cognitive and manipulative abilities of early hominins.[77,78,80]

Conclusion

The combination of dexterous extractive foraging, innovative tendencies, individual and social-learning abilities, and conditions conducive to social learning is known to favor the emergence of habitual tool use. Here, we add terrestriality as an important explanatory variable, which improves the explanatory power of the preconditions for the evolution of habitual and complex tool use among nonhuman primates (see Fig. 3 and Meulman and van Schaik[4]). Terrestriality may therefore have been an important facilitator of flourishing of hominin technology, which is commonly argued to be the driving force behind hominin intelligence.[81] The terrestriality effect arises because it creates enhanced opportunities for innovation, accumulation, and social learning, and in doing so favors cultural intelligence.[49,82] Thus, terrestriality may boost innovative and social-learning abilities beyond what is possible in arboreal habitats and appears to have been crucial for the emergence of cumulative material culture.

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CHAPTER 4

Prosocial tool transfers in wild great apes? *Implications for the evolution of technology*

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Abstract

Background Humans are unique in their cooperative nature and their proactive prosocial behavior. Cooperative breeding has been proposed to explain the near absence of such proactive prosocial tendencies in our closest relatives, the great apes, but lack of inhibitory control in foraging contexts is a plausible alternative. This study aims to distinguish between these alternative explanations by studying transfer interactions involving non-food items, tools, in *Pan troglodytes troglodytes* and *Pongo abelii*.

Results. We find that tool transfers are rare in general, with higher percentages observed for terrestrial tool-using chimpanzees than chimpanzees using tools in arboreal settings or arboreal orangutan tool users. Proactive tool transfers were absent overall, reactive tool transfers were only observed for chimpanzee termite gathering (terrestrial context), and passive transfers were observed for chimpanzees in terrestrial and arboreal (i.e. honey dipping and leaf sponging) contexts. Protested transfers (not prosocial) were the only types of transfers observed for the arboreal orangutans.

Conclusions. This study shows a lack of proactive prosociality in large-brained great apes, even toward close kin, in a context not directly involving food. Terrestriality may partly compensate for this lack and, in combination with cooperative breeding, may have helped our hominin ancestors to overcome this great-ape constraint and develop a rich cumulative cultural behavioral repertoire unique among animals.

Highlights

- Wild great apes show no signs of proactive prosociality during tool-using events, even toward offspring.
- ... higher tolerance of reactive transfers in terrestrial than arboreal contexts …
- Terrestriality may have partly compensated for the lack of proactive prosociality …
- ... terrestriality and cooperative breeding allow for cumulative culture

Introduction

Prosocial behaviors are acts of help or assistance to others, such as grooming, food sharing, allomaternal care, teaching, territorial and predator defense, coalitionary aggression, or cooperative hunting [1-3]. All primates exhibit such prosocial behaviors [1, 3-7], but the mechanisms underlying these transfers may differ across species. When the prosocial acts involve sharing of commodities, tools or information, owners may share proactively, reactively, or passively [8]. In proactive sharing, transfers are initiated by the owner in the absence of any soliciting stimuli. In reactive sharing, owners actively give or facilitate taking in response to specific stimuli, such as solicitation in the form of begging. Finally, in passive sharing, the owner is passive but tolerant. When food is taken from the owner, we do not speak of prosocial sharing (see Table 1).

Table 1 Definitions of transfer interactions [modified from 8].

Category	Type of transfer	Prosocial? (tolerance)	Definition
Proactive	Offering	Yes	Owner initiates transfer without request by recipient
Reactive	Active sharing/ Facilitated taking	Yes	In response to begging, owner actively transfers the tool and/or makes movements conducive to transfer
Passive	Relaxed claim/ Tolerated taking	Yes	Owner allows recipient to take the tool
Passive	Forced claim	No	Recipient takes the tool despite resistance by owner
Passive	Steal	No	Recipient snatches tool by surprise, preventing resistance by owner

Great apes have so far been found to be almost exclusively reactively or passively prosocial in food-sharing contexts [8-15]. Humans, in contrast, seem to have a unique prosocial motivational predisposition to proactively share food in the form of active provisioning [16, 17]. Indeed, we even proactively share mental states with others, which we use systematically in cooperative contexts, a capacity also referred to as "shared intentionality" [18-20]. This derived human hyper-sociality has been argued to underlie many of our unique cognitive achievements such as language, symbol use, technology, social norms and institutions, religion, and large structurally complex societies [20, 21]. Because among primates, only the cooperatively breeding primates (e.g. *Callitrichidae*, and to a lesser extent *Cebus*), show a similar motivation to engage in proactive prosocial behavior [22-24], the cooperative-breeding hypothesis proposes that humans acquired this predisposition through their switch to cooperative breeding [20, 21].

The conclusion that humans and the other great apes have different proximate mechanisms underlying prosocial behavior is largely based on experiments. Human prosociality has mainly been studied through economic games in which individuals were tested anonymously (excluding reputation effects as much as possible) for their intrinsic motivation to share (i.e. without any known reciprocal benefit) [10, 25, 26]. Great ape prosociality has mainly been tested via provisioning games. Therefore, rather than being due to the absence of cooperative breeding, the near-absence for proactive prosociality in great apes could alternatively be an artefact explained by an obsession with, and a reluctance to give up, valuable food items [8, 10, 11, 27-31].

If indeed the lack of proactive prosociality in the ape experiments is due to such an obsession with food, we would expect great apes to show more proactive prosociality in contexts that do not directly concern food. For example, great apes may proactively transfer tools, as these are only indirectly associated with food, much like tokens in experimental settings [cf. 28, 32]. The tool-use context might thus facilitate proactive prosocial transfers in

great apes. If this alternative interpretation holds, we must question the inferred evolutionary origins of the human capacity for shared intentionality.

As with the transfer of food, tool transfers may be proactive, reactive or passive. The available captive studies suggest that prosocial transfers in the tool-use context are largely reactive or even passive [11, 30, 33]. However, the design of experimental studies may bias toward one or the other form of prosociality (for instance, in targeted helping, proactive tool transfer is impossible). Moreover, no study has explicitly focussed on tool-transfer interactions in the wild, where acquiring tool use may be more critical [34-37]. Immature great apes acquire complex extractive-foraging techniques, in particular when tool-assisted, through a lengthy process of social learning and individual practice, in the form of peering and affordance learning following food transfer [34-37]. Thus, tool affordance learning in particular, would benefit from the active (proactive, reactive) transfer of tools [38, 39]. Indeed, some studies in natural settings suggest proactive prosociality. There are, for instance, cases of active instruction [40] and of opportunity teaching [34, 41], where the mother delays her nut cracking while the infant manipulates her nut-cracking tools [41]. However, in other populations mothers only passively share tools by readily allowing offspring to take them [33, 40], or immatures even steal tools to acquire them [35]. Finally, tools transferred between mature chimpanzees in the wild typically involve tool recovery or passive tolerance of tool taking, and occurs in different social contexts [42]. Overall, then, in both wild and captive apes, tool transfers, like food transfers, may range from being proactive to being reactive or even passive. However, to date a systematic study of tool transfers among wild great apes is lacking. The present study is thus aimed at helping to resolve the nature and evolutionary functions of hominid prosociality.

The aim of this study is to establish whether evidence for proactive prosocial donation in great apes exists for non-food items, in the form of active transfer of suitable tools to learners. We systematically analyzed observational data and video recordings, focusing

specifically on tool-sharing behaviors in common chimpanzees (*Pan troglodytes troglodytes*) and Sumatran orangutans (*Pongo abelii*).

We find no evidence for proactive tool transfers among either species, but notable interspecific variation in the actual rate of tool transfers, which may be attributed to the contrasting settings (arboreal versus terrestrial). These results seem to be consistent with the conclusion that shared intentionality is built on a novel psychological platform of cooperation. Terrestriality, however, may have partly compensated for this lack of proactive prosociality in chimpanzees by inducing tendencies for reactive prosociality. Further studies are needed to confirm such an effect of a terrestrial tool-use context.

Results

Before we compare the tool-transfer interactions observed for the two great ape species, we will first describe the main results per species and type of tool use.

Chimpanzees

Termite-gathering Tools. Three types of tools (fishing probes, perforating twigs, and puncturing tools) were used by the chimpanzee population to gather termite prey [43]. Within 29.3 hours of remote video recordings of chimpanzees at termite nests, fishing probes, or materials to manufacture fishing probes, accounted for 84% of the observed tools (n=299), with perforating twigs (n=30) and puncturing tools (n=30) each accounting for 8% of our tool observations. Although within this data set we only observed the transfer of fishing probes, we have also directly observed passive transfers of perforating and puncturing tools within this chimpanzee population.

We documented 17 tool-transfer interactions (see Table 2, Figure 1). None of the transfers were proactive, but most (11/17= 65%) were nonetheless prosocial, occurring through reactive transfers in response to begging (n=6) or passive transfers in the form of tolerated taking (n=5). The remaining incidents of passive transfers were not prosocial, but

occurred as a result of stealing (n=1) or forced claims (n=5). Tool-transfer interactions were most commonly observed among mothers and their immature offspring. Juveniles were most effective in gaining tools from others (see Table 2). Furthermore, more than half of the observed tool transfers (9 of 17 transfers, 53%) also involved gaining access to a termite tunnel for fishing, suggesting that youngsters also gained access to those parts of the tool-use sequence that led directly to foraging.

Out of the total of 357 tools, 258 tools (72%) were used within 10 meters proximity from another conspecific. In 38 cases the conspecifics within 10 meters showed interest in the tool user (i.e. in the form of watching the tool user, or food-transfer interactions), Nevertheless, despite interest, no tool-transfer interaction was observed in 21 cases (see Figure 2).

Honey-gathering Tools. We documented 30 tools used in honey gathering, representing four different tool types (Pounding clubs, n=20; Dipping sticks, n=7, Levering tools, n=2, Swatting tool, n=1). Nine of these tools (30%) were used within transfer proximity (10 meters) from another conspecific (Figure 2). Interest by a conspecific was shown on seven instances, one of which resulted in a tool transfer (Table 2, Figure 1). The tool transfer involved a request by an adult female toward a juvenile's tool used to pound a bee hive, and resulted in a forced claim (see Table 2).

Leaf-sponging Tools. Twenty-five leaf-sponging tools were observed during our study. There was potential for tool transfer in three cases (12%), with interest in the tool use being shown by a conspecific on two occasions (Figure 2). The tolerated taking of a tool by an infant male from his older subadult brother was observed on one occasion (Table 2, Figure 1).

Orangutans

During a total of over 6,500 hours of observation over two years, we observed over 52 hours of feeding sessions in which tree-hole or seed-extraction tools were used for more than 15 hours (since tool use was alternated with feeding without tool in these feeding sessions). Out of a total of 151 tools that were used, 126 were used by independent individuals. Tool-transfer interactions were observed for only three tree-hole tools (corresponding to two tool sessions), of which two resulted in a successful transfer of the tool (and feeding site), whereas one was refused (see Table 2). For 80 of the 151 tools (53%) tool transfer was possible because there were conspecifics within 10 meters (see Figure 2). For 38 of these tools, there was no interest, despite the potential for transfer. For 39 tools, no tool-transfer interaction was observed, although potential recipients did show interest (i.e. by peering the tool user, begging for food acquired by the tool user, or feeding at the feeding site simultaneously or after the initial tool user left).

Two of the three tool-transfer interactions occurred during a single feeding session in which a mother, her male infant, and a female adolescent (probably her weaned daughter) were feeding in the same tree, initially on flowers of *Tetramerista glabra* (Miq.). The tree-hole tool use started when the young infant started to break off a branch. The mother broke the branch further and started feeding with a tool, on ants inside the stump that was left behind. The infant immediately started peering and begging, and tried repeatedly to take the tool from his mother. After 4'45" the mother stopped resisting and tolerated the infant to take the tool from her mouth. She subsequently left the feeding site, after which the infant took over. Shortly afterwards, the older sister approached her younger brother. She almost instantly started making a tool herself, after which she took over the feeding site and started using the tool. Her younger brother watched her (i.e. peered) and repeatedly tried to take the tool from his sister. After 6'32" he succeeded (because his sister gave up resistance), after which the sister left and the younger brother could take over the feeding site again. All three individuals

continued feeding on flowers in the same feeding tree after their tool use. Both tool-transfer interactions are examples of non-prosocial transfers (forced claims after multiple refusals - protested), followed by a feeding-site transfer (see Figure 1).

The other tool-transfer interaction occurred while the same mother and infant were in proximity of an adult unflanged male feeding with a tool from a tree hole. Both the mother and infant peered at him using the tool. After one minute the infant reached for the male's tool but the unflanged male refused and chased him away. The male continued feeding for about half an hour while mother and infant peered at him (again) and occasionally begged for or took some food. Then the male "stepped aside" after which the mother took over the feeding site and made a new tool for herself. The male watched her for a couple of minutes and then moved away (following another conspecific). The infant then peered at his mother while she was feeding with the tool. After circa 5 minutes the mother moved away as well, whereupon the infant started feeding from the tree hole by hand. Shortly afterwards, the infant also moved away, following his mother. Earlier observations (1993-1999) had also yielded a few cases of unsuccessful attempts by infants to take tools form their mothers (CvS, unpublished).

Tool-transfer interactions across species and contexts

The results described above indicate that tool-transfer interactions are not that common among chimpanzees (termite gathering: 17/357 tools=4.8%, honey dipping: 1/30 tools =3.3%, leaf sponging: 1/25 tools =4.0%) or orangutans (3/151 tools =2.0%). Proactive transfers were not observed at all and reactive transfers were only observed for chimpanzee termite-fishing tools (n=6). Tolerated takes (passive transfers) occurred only for tools used by chimpanzees, in terrestrial as well as arboreal contexts (termite gathering: n=5, leaf sponge: n=1). The remaining transfers were not prosocial, but amounted to forced claims (chimpanzees: termite gathering n=5, honey dipping n=1, orangutans: n=3) or stealing events (chimpanzees: termite gathering n=1). Forced claims were thus the only type of transfers observed in orangutans.

Table 2 Details tool-transfer interaction data

Species	Context	Tool Type	Transfer Type	From	To
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Reactive-active	AF	SA
Chimpanzees	Terrestrial	Termite Fish	Tolerated taking	AF	INF
Chimpanzees	Terrestrial	Termite Fish	Tolerated taking	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Tolerated taking	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Tolerated taking	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Tolerated taking	AF	SA
Chimpanzees	Terrestrial	Termite Fish	Forced claim	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Forced claim	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Forced claim	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Forced claim	AF	JUV
Chimpanzees	Terrestrial	Termite Fish	Forced claim	SA	INF
Chimpanzees	Terrestrial	Termite Fish	Steal	JUV	INF
Chimpanzees	Arboreal	Leaf Sponge	Tolerated taking	SA	INF
Chimpanzees	Arboreal	Honey Pound	Forced claim	JUV	AF
Orangutans	Arboreal	Tree hole	Forced claim	AF	INF
Orangutans	Arboreal	Tree hole	Forced claim	JUV	INF
Orangutans	Arboreal	Tree hole	Forced claim*	AM	INF

Notes
* Refused and thus unsuccessful claim that did not result in an actual transfer. AF=adult female, AM=adult male, SA=subadult, JUV=juvenile, INF=infant.

Figure 1 shows these results and additionally shows the proportion of tools for which no tool-transfer interaction occurred despite conspecifics showing interest (chimpanzees, termite gathering: 55.3%; honey dipping: 85.7%, n=7 and leaf sponging 50.0%, n=2, pooled: 78%; and orangutans: 92.9%). Statistical analyses showed that in cases where interest is shown tool transfer was far more likely in chimpanzee termite gathering than orangutan tool use (Pearson Chi-square= 15.038, n=80, df=1, $p<0.001$). Arboreal chimpanzee tool use (for which the honey-dipping and leaf-sponging data were pooled together) were intermediate and did not differ significantly from either the terrestrial termite-fishing context in chimpanzees or the arboreal orangutan tool use (Pearson Chi-square= 1.532, n=47, df=1, p=0.278, or Pearson Chi-square= 1.906, n=51, df=1, p=0.209, respectively).

To interpret the significant difference in tool-transfer interactions between arboreal orangutan tool use and terrestrial chimpanzee tool use, we also examined the social context at the time of tool use (see Figure 2). The three groups of tool contexts, that is "terrestrial chimpanzee tool use", "arboreal chimpanzee tool use", and "arboreal orangutan tool use" differed significantly in the frequency with which tool-use events were observed within 10

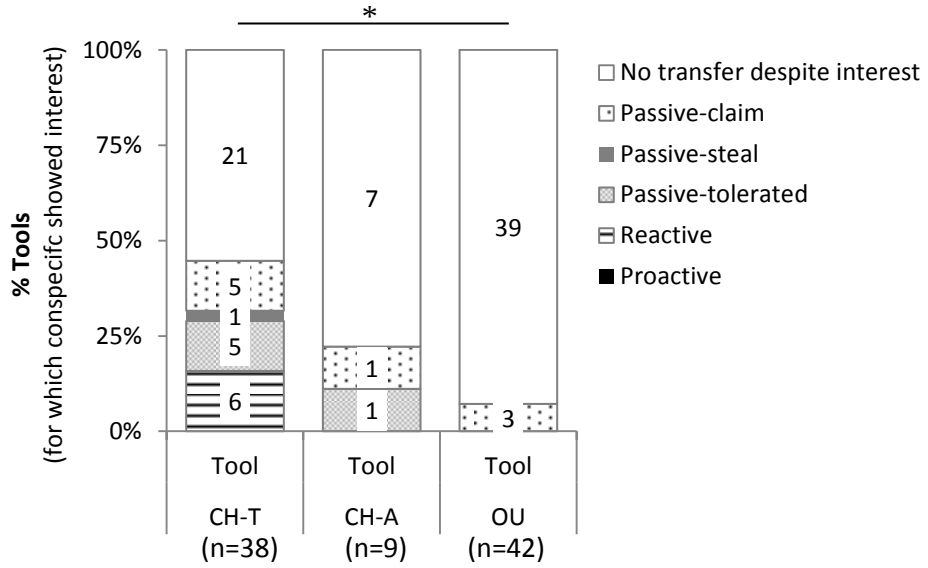

Figure 1 Type of tool-transfer interactions. Each type is shown as a percentage of the total number of tools conspecifics showed interest for. The data labels represent the number of tools associated with these percentages. The ratio between "interest but no transfer interaction" versus "interest and transfer interaction" differs significantly between orangutan tool use and chimpanzee termite gathering (Pearson Chi-square= 15.038, n=80, df=1, p<0.001). Arboreal chimpanzee tool contexts, mainly driven by honey dipping, were intermediate and did not differ significantly from terrestrial termite gathering in chimpanzees or arboreal orangutan tool use.

meters from another conspecific. Biases were found to be in favor of chimpanzee tool use in terrestrial context and against arboreal chimpanzee tool use, with arboreal orangutan tool use being intermediate (see Figure 2b). Additionally, those conspecifics that were within 10 meters showed significantly more interest for tools used in arboreal than terrestrial contexts (Pearson Chi-square= 59.260, n= 350, df= 1, p< 0.001; Figure 2c). Hence, although the observed differences in tool-transfer interactions between orangutans and chimpanzees could be due to a species difference, alternatively these results are consistent with effects of terrestriality.

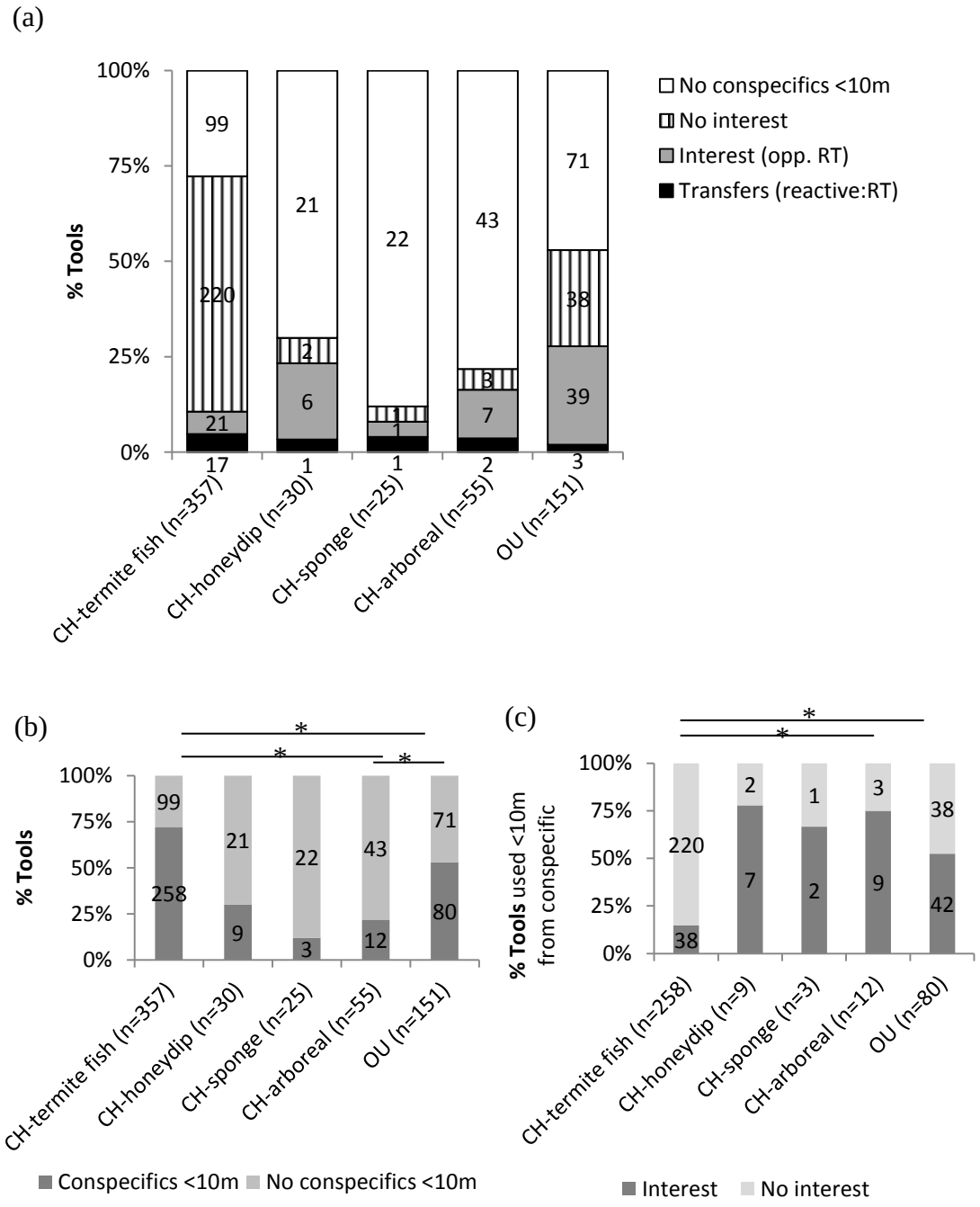

Figure 2 Social context in which tool use was observed. Data are shown for three groups of tool contexts: "terrestrial chimpanzee tool use", "arboreal chimpanzee tool use" (i.e. (honey dipping and leaf sponging were pooled into one arboreal tool category for chimpanzee tool use), and "arboreal orangutan tool use". Figure (a) gives an overall picture of all the tools used. Figure (b) examines whether or not conspecifics where around (within 10 meters) when tools were used. Figure (c) illustrates for which of the tools used when conspecifics were around, these also showed interest in the tool user by watching, begging for food or tools, or by (co-) feeding from the same feeding site. Significant differences were found for the ratio of tools used when conspecifics were within 10 meters (chimpanzee terrestrial – arboreal: Pearson Chi-square=53.705, n=412, df=1, $p<0.001$; chimpanzee arboreal tool use - orangutan tool use: Pearson Chi-square=15.840, n=206, df=1, $p<0.001$; and chimpanzee terrestrial tool use - orangutan tool use: Pearson Chi-square=17.732, n=508, df=1, $p<0.001$).

When within 10 meters conspecifics showed interest for significantly fewer tools that were used in terrestrial context by chimpanzees than tools used in arboreal context by chimpanzees (Pearson Chi-square=28.972, n=270, df=1, $p<0.001$) or tools used by arboreal orangutan (Pearson Chi-square=48.222, n=338, df=1, $p<0.001$).

Discussion

Proactive prosociality and teaching via tool transfers

The main finding of this study is that we observed no signs of proactive prosociality in the two great ape species during tool-using events. For both chimpanzees and orangutans, the transfers were reactive or passive and did not include any proactive offering. Particularly in the termite-gathering context, mature chimpanzees showed a high degree of tolerance toward the requests of younger individuals and assumed costs from relinquishing their tools to conspecifics. The transfer of tools, as a potential form of non-food prosociality, is therefore rare and just as reactive or passive as the transfer of food in these great apes (see Figure 3). Accordingly, we conclude that the near-absence of proactive prosocial behaviors in great apes in the food context are not a consequence of a lack of inhibitory control specific to this context, as suggested previously by various authors [8, 10, 11, 27-31]. In contrast, the findings are in complete agreement with the rare occurrence of proactive sharing in great apes, in contrast to humans [11, 22, 33, 44]. Teaching can be seen as proactive information donation, and thus is a form of proactive prosociality. In our tool transfers, there was no sign of teaching. The findings are therefore consistent with the cooperative-breeding hypothesis, which argues that proactive sharing (including active teaching) should only be expected in cooperative breeders (aside from some rare events in apes) because of their unique psychological predisposition for proactive prosocial behavior [10].

How terrestriality may affect prosociality

We observed remarkable species and context differences in the amount of tools used when conspecifics were nearby, the interest these conspecifics showed, and the number of tool-transfer interactions. First, arboreal tool use in chimpanzees appears to be a more solitary activity than terrestrial tool use in chimpanzees or arboreal tool use in orangutans. Second, there were significant differences in the level of interest shown by conspecifics according to context and species, in favor of arboreal contexts and orangutans as opposed to terrestrial contexts and chimpanzees, respectively.

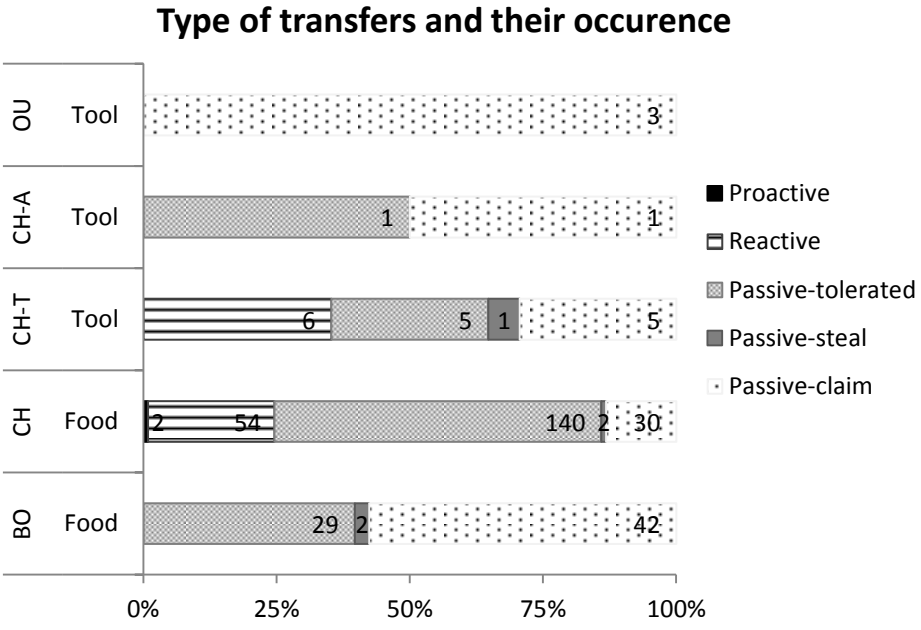

Figure 3 Food- and tool-transfer interactions compared in terms of types of transfer interactions [as reported by 8].

Species differences in lifestyle could have caused the differences in tool-transfer interactions and social settings. Indeed, chimpanzees in arboreal contexts were behaviourally more similar to arboreal orangutans than chimpanzees in terrestrial contexts, in that there were fewer tool-transfer interactions, reactive prosociality was absent, higher levels of interest from conspecifics and perhaps lower tolerance levels of tool owners. Because tools used on

the ground are often more complex [cf. 39], the greater need for tool-affordance learning may be reflected in more tool-transfer interactions, reactive prosociality and tolerance to claims. Additionally, tools that are dropped by tool owners after use disappear in the undergrowth in arboreal contexts, whereas they remain salient and close by when used and dropped in terrestrial contexts. Especially in the absence of proactive prosociality, and even more so when reactive prosociality and tolerance are also absent, such indirect tool transfers may offer the only opportunity for tool affordance learning, and may thus be especially crucial for more complex tool use and cumulative technology [45-47]. Terrestrial tool contexts and lifestyles may therefore be associated with higher levels of tolerance, and more opportunities for claims and positive reinforcement via indirect tool transfers, which may explain the higher rates of tool-transfer interactions observed for chimpanzee termite gathering, as opposed to arboreal use of tools by chimpanzees or orangutans. However, larger sample sizes and future studies are needed to confirm whether such a potential effect of terrestrial contexts on tool use exists.

Conclusion

This is the first systematic study of wild great apes to show that the lack of evidence for proactive prosociality in wild great apes is not due to their lack of inhibitory control in foraging contexts, because proactive prosociality is also absent in tool-use settings, a context not directly related to food, but the very context in which such acts would have been particularly beneficial (high quality food, complex skills and high learning costs). The higher tolerance of reactive transfers in terrestrial rather than arboreal contexts suggests that terrestriality may enhance tendencies toward reactive prosocial behavior in tool-using great apes [39, 48]. This study provides important insights into the evolutionary constraints acting on the large-brained great apes and into the conditions that helped our hominin ancestors to overcome these constraints (i.e. terrestriality and cooperative breeding) to allow for cumulative culture and proactive prosociality.

Experimental procedures

Study Sites. Chimpanzee observations were conducted in the Goualougo Triangle, located in the southern section of the Nouabalé-Ndoki National Park (16°51′−16°56′ N;

2°05′−3°03′ E), Republic of Congo. The study area encompasses 380 km^2 of evergreen and semi-deciduous lowland forest, with altitudes ranging between 330 and 600 meter. Rainfall is bimodal, with a main rainy season from August to November and a short rainy season in May. Orangutan data was collected at the Suaq Balimbing Research Station (3° 02.873' N, 97° 25.013' E) in the South Kluet Region of the Gunung Leuser National Park, near Sumatra's west coast in the south of Aceh, Indonesia. The 350 ha study area is dominated by lowland peat swamp forest with patches of dipterocarp hill forest at the eastern boundary, and the Lembang River with adjoining rattan thickets and regularly flooded back swamps at the western boundary.

Data Collection. For the chimpanzees, remote video recording devices with passive infrared motion sensors were used to conduct surveillance at termite nests for visitation and tool using behaviors. Detection of movement by the sensor caused the camera to record for two-minutes intervals until triggers ceased [43]. For the orangutans, focal animal follows were conducted from night nest to night nest, recording all social and tool-related behaviors continuously. Video recordings were used to confirm observations when possible. Tool-transfer interactions were only recorded as such when the actual transfer of the tool was observed. Cases of doubt were excluded.

Definitions. Tool events were recorded as having a sharing potential when another individual was within 10 meters or within the same feeding tree as the tool user. A tool-transfer interaction occurred when one individual took or attempted to take possession of another individual's tool. Proactive transfers involved the owner giving the tool to another without receiving solicitation, whereas reactive tool transfers involved the active transfer of a tool by its owner in response to begging. Begging in this context was defined as soliciting a tool from another individual. Additionally, passive sharing could occur (initiated exclusively by the recipient). Different types of passive transfer could occur depending on the tolerance of the owner (i.e. tolerated/relaxed claims, hesitant/protested transfers – including refused transfers, or stealing). Interest, in the absence of tool-transfer interactions, could be expressed by watching or begging for food. Watching included all peering [see for definitions 49] and

peering-like watching within 10 meters. Begging for food included all attempts of soliciting for or taking food from the tool user or the tool-use site the tool-user was feeding from.

(Video) Data Scoring and Analysis. The chimpanzee data from the digital video cassettes were archived on external hard drive devices and converted to MPEG files for review. Video analysis was conducted using INTERACT Version 9 [50]. Twenty-nine hours of the remote video archive were searched for tool-transfer interactions. Inter-observer reliability between two coders on tool transfer definitions (see following section for definitions) was excellent (94% agreement, n=34 episodes). In addition, 55 instances of tool using behavior in honey gathering and leaf sponging were digitally recorded with handheld cameras during reconnaissance surveys of chimpanzees. Orangutan data has been processed and analyzed in excel 2007 and SPSS 18.0. Video recordings were additionally watched to identify occasions of tool-transfer interactions. These transfer interactions were subsequently digitalized, converted into avi format, and analyzed using INTERACT Version 9 [50]. In total 57 sessions of orangutan tool use (seed-extraction and tree-hole tool use) were observed over a two-year period (June 2007- June 2009), including 118 tools. Data, as well as video recordings, were analyzed for the occurrence of tool-transfer interactions as described above for the chimpanzees. We identified only three tool-transfer interactions for which the inter-observer reliability was 100%.

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CHAPTER 5

If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use

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Abstract

Many species use tools, but the mechanisms underpinning the behaviour differ between species and even among individuals within species, depending on the variants performed. When considering tool use 'as adaptation', an important first step is to understand the contribution made by fixed phenotypes as compared to flexible mechanisms, for instance learning. Social learning of tool use is sometimes inferred based on variation between populations of the same species but this approach is questionable. Specifically, alternative explanations cannot be ruled out because population differences are also driven by genetic and/or environmental factors. To better understand the mechanisms underlying routine but non-universal (i.e. habitual) tool use, we suggest focusing on the ontogeny of tool use and individual variation within populations. For example, if tool-using competence emerges late during ontogeny and improves with practice or varies with exposure to social cues, then a role for learning can be inferred. Experimental studies help identify the cognitive and developmental mechanisms used when tools are used to solve problems. The mechanisms underlying the route to tool-use acquisition have important consequences for our understanding of the accumulation in technological skill complexity over the life course of an individual, across generations and over evolutionary time.

1. Introduction

Research over the past two decades has shown that tool use (for definition see: [1, p. 5]) is not as rare among non-human animals as we once thought [1]. Tool use in natural settings nevertheless remains restricted to only a minority of animals that mostly express the behaviour incidentally rather than routinely. Although studies on incidental tool users can be useful in determining factors influencing behavioural innovations, they would provide us with little insight on the adaptive value, evolution or cognitive underpinnings of tool use. Routine tool users, on the other hand, provide us with opportunities to study ontogeny and individual variation which can help to elucidate the level of phenotypic plasticity and cognition underlying the behaviour.

Routine tool users are often classified as either customary (or universal) or habitual, based on geographical variation in the trait. Although habitual tool use is often considered to be the product of social learning, this inference is usually based on the problematic exclusion method (i.e. elimination of environmental or genetic causes of variation). However, we propose that both longitudinal and experimental studies on tool-use development and individual variation can assist in identifying underlying mechanisms and cognitive underpinnings of habitual tool use. As such, we confine ourselves to the cases of habitual tool-assisted foraging as reported by Shumaker et al. [1]. We advocate similar lines of study for other cases of routine tool use (i.e. more customary/ universally prevalent forms of tool use, such as we find in humans), before we can try to unravel potential selective pressures on tool use and cognitive evolution.

(a) Habitual tool use

In cataloguing variation in tool repertoires of wild chimpanzee populations, McGrew went beyond the simplistic categorization of ‘present’ versus ‘absent’ tool variants by additionally distinguishing between ‘habitual’ versus ‘rare, idiosyncratic or questionable’ tool use. He defined habitual tool use as tool-use patterns shown repeatedly by several members of a group; excluding single instances by one or several individuals, several instances by only one individual and all instances of insufficient data or involving released animals [2, p. 180]. Subsequently, Whiten et al. distinguished between ‘customary’, ‘habitual’, ‘present’, ‘absent for ecological reasons’, ‘absent for no apparent ecological reason’, and ‘unknown’ and redefined ‘habitual’ as ‘behaviour that is not customary (i.e. occurring in all or most able-bodied members of at least one age–sex class) but has occurred repeatedly in several individuals, consistent with some degree of social transmission’ [3, p. 682]. This definition

also applies to our use of the term ‘habitual tool use’. McGrew emphasized that the definition of ‘habitual’ leads to an incomplete tool catalogue of habitual tool variants for most populations owing to the positive correlation between study length and number of identified habitual tool-use variants. Whiten et al. [3] thus focused on the importance of: (i) making tool catalogues more complete; (ii) clarifying the extent to which a variant is habitual; and (iii) systematically documenting behavioural variants absent in a particular population but present elsewhere.

In view of this geographically based categorization, habitual tool use has been set aside from other forms of (routine) tool use that are, for example, customary, idiosyncratic or absent in some sites owing to ecological or genetic variation. Accordingly, in contrast to these other forms of (routine) tool use, habitual tool use has been suggested to depend on cognitive flexibility that enables animals to solve disparate problems and use social cues, rather than rely on predisposed action patterns that are comparatively fixed [3,4]. However, the supporting data that these tool users invent and other individuals within the population then socially learn their techniques is rarely definitive and open to alternative explanation [4–6]. First, the distinction between habitual and ‘absent due to no apparent ecological reasons’ is problematic. Not only is it logically impossible to demonstrate the absence of a cause, in the end only a small portion of the potentially relevant factors can be realistically considered, even without including possible interaction effects. Second, to some extent, ecological factors always influence the expression of behavioural phenotypes, so why bother to exclude them at all? When trying to exclude genetic factors or individual learning, similar problems arise. Langergraber *et al.*, for instance, showed that, for chimpanzees, geographical variation correlated strongly to genetic variation, leaving only a few behaviours (ca 13%) for which expression varied geographically among genetically similar groups [6]. Third, when no geographical variation is found, behaviours might still be socially learned. Tool-use preferences in sea otters (Enhydra lutis), in terms of type of prey, tool-use method and foraging strategy seem, for example, to be vertically transmitted even though the use of rocks to open or dislodge hard-shelled food is common for all sea otters and does not seem to require social learning [7]. Fourth, when behaviours can be acquired exclusively by individual learning, this does not mean that they are. Simple Pandanus and twig tool use in New Caledonian crows is, for instance, influenced by social input even though correct performance can also be acquired without social cues [8,9].

Geographical variation in tool use is thus an indirect and possibly problematic route to evaluate the degree to which habitual tool use relies on social learning and reflects general

cognitive abilities. Instead, it would be more productive to establish whether we can find any direct evidence for social learning and general cognitive abilities. In the case of the woodpecker finch, for example, observational as well as experimental lines of inquiry point toward strong genetic and ecological influence in shaping the form and expression of tool use. Experimental evidence moreover reveals that presence of social cues does not seem to have any effect [10], while cognitive strategies shared with non-tool-using relatives appear to underlie the use of tools [11]. What about the so-called 'habitual tool users' as classified by Shumaker et al. [1]: bottlenose dolphins (*Tursiops sp.*) [12], sea otters (*E. lutis*), orangutans (*Pongo sp.*) [4], chimpanzees (*Pan troglodytes*) [13–15], capuchins (*Sapajus sp.*) [16,17], Burmese long-tailed macaques (*Macaca fascicularis aurea*) [18,19],[1] New Caledonian crows (*Corvus moneduloides*) [9,20], and possibly green-backed herons (*Butorides sp.*) [21]?

In this article, we review studies that directly examine the development of habitual tool use over life history and compare its emergence to other 'tool-free' foraging behaviours. We explore three different lines of evidence that contribute to our understanding of habitual tool use: (i) observational data of acquisition patterns; (ii) experimental evidence illustrating cognitive challenges associated with tool use; and
(iii) individual differences revealing the role of social input in the wild. We discuss the implications that this analysis of tool ontogeny might have for uncovering the cognitive mechanisms underpinning tool use in different species and some possible directions for future work. For the purpose of this paper, we focus on foraging tools and skills because of their direct link to survival and fitness.

2. Observational field studies reveal typical tool-acquisition patterns

(a) Practice and errors

Observational field data indicate that habitual tool users take almost their entire developmental period to acquire tool competence for the relevant tool variant. By competence, we mean regularly succeeding in achieving the goal (here, obtaining food). Table 1 shows that for several species, some behaviours are not acquired until years after the animals are able to forage for themselves without tools. A preliminary comparison of other

[1] Not much known yet on individual variation or skill acquisition (but see [18,20]).

routine or non-tool users and habitual tool users also suggests a relative late age at skill competence for habitual tool users (figure 1). Sea otters appear to be an outlier among the habitual tool users in acquiring tool competence relatively fast; whereas spotted hyaenas and wolves appear to be outliers among the non-routine tool users because they acquire their skills (i.e. hunting skills) relatively late. Hunting skills are indeed often considered complex, requiring more learning (see also [55]). What are immatures doing during this period? Why the delay? Are they not yet motivated to carry out these possibly more costly foraging skills (in terms of time, and sometimes physical effort), while they are still physically immature and provisioned by their parents? In most observational studies reviewed, immatures spend a good deal of time interacting with tool material before they are competent [17]. What can detailed analysis of their behaviour tell us about the possible development of cognitive adaptations that may underpin the adult behaviour?

Many, though by no means all, habitually used tool behaviours are associated with a long period during which immatures interact with the tools and the goal objects, but use a characteristic pattern of non-random 'errors': either the wrong action or tool material, an incomplete action sequence, action sequences performed in the wrong order, or the correct complete and ordered action sequence applied towards the wrong goal or substrate. For example, Pandanus tool competence in New Caledonian crows progresses according to four probing techniques and five manufacturing techniques, of which only the fourth probing and fifth manufacturing technique resemble adult-like competence, which takes on average seven months to master. Adult-like proficiency (i.e. efficiency, speed, etc.) is acquired even later (ca. 12 months). All other probing and manufacturing techniques include errors that result in faulty detachment or dysfunction of the tool [9]. Capuchins in Tiete (Sapajus apella) go through eight developmental stages across 2.5 years before mastering their nut-cracking skills, from simple manipulation, to rubbing or hitting objects, to inserting in and hitting against substrates, striking objects against anvils and eventually placing nuts on anvils, followed by ineffective nut cracking before effective nut cracking. On rare occasions, individuals bang two detached objects together [56]. Gombe chimpanzees start with pressing a tool to the termite mound or swiping the mound (at 3.5 years), and gradually change this into haphazard, rapid tool insertion without the required depth (4.5 years), to successful termite fishing (5.5 years) [42]. Although evidence for such 'errors' is still missing for bottlenose dolphins, orangutans, sea otters and long-tailed macaques, anecdotal evidence and studies on macaque stone handling suggest similar paths of development [22,57,58].

As to how far the 'errors' observed during the developmental period actually represent goal-

directed attempts instead of random play or exploration is difficult to establish. However, errors diminish over time while tool-using skills improve, until eventually adult-like competence is reached before or around weaning age [9,42,44,59,60]. Nonetheless, compared to adults, competent weaned immatures often still show inadequate skills by persisting at unrewarding locations, using tools at successful locations less often, having shorter or longer lasting tool sessions than adults, using more tools per session, modifying tools more frequently, using tools with different features (material, size and shape) than adults or— only relevant in some contexts—lacking hand preferences [9,18,35,41,44,59,60]. Hence, although we might have mischaracterized play and exploration as 'errors', the 'error-filled' period of practice does seem to eventually result in skill improvement, whether actively goal-directed or facilitated by exposure to ecological and/or social factors.

Of course, development, physical maturation and changing motivation coincide (e.g. with regard to foraging strategies, social interactions, perception and coordination). Physical maturation thus probably contributes to, but cannot fully explain the delays and errors in tool-using competence. For example, the random instead of routine tool use at younger ages suggests lack of systematic coordination rather than physical strength. Given that individual variation in competence often varies with learning opportunity (with some immatures performing even better than some adults, see §4), we suggest that opportunities for learning, not maturation, is the primary limiting factor. Age might even constrain learning ability if a sensitive period of exposure has passed [10,61]. **(b) Phenotypic biases**

The discrepancy between adult and immature tool behaviour described above (or see table 1) may also tell us something about the predisposed phenotypic biases a species may have that may either promote or constrain innovation and/or acquisition of tool behaviours. Both physiological traits (e.g. lack of appendages for manipulation) and behavioural biases are informative, especially when contrasted with closely related species (see §3a). Such phenotypic biases provide guidance with respect to which tool-mediated behaviours are relatively fixed (i.e. genetically hard-wired), as opposed to those that require extensive learning and social input, assuming ecological learning opportunities are present. For instance, North American badgers (Taxidea taxus) frequently capture hibernating squirrels underground and are morphologically and behaviourally specialized to excavate burrow systems by the movement of soil [62]. Hence, the use of soil to plug openings into burrow systems occupied by ground squirrels may be considered an idiosyncratic expression of their normal behaviour, also because opportunities for social transmission are rare. Similarly, sea otters show a strong genetic predispositions for increased tactile sensitivity of the hand [7]

Table 1 The time course of emergence for several habitual tool behaviours in different species relative to other developmental hallmarks. (Columns 2–8 give the average age (in months)a of sexual maturity, weaning/fledging, first foraging attempts, first object manipulation, competent 'tool-free' foraging on simple food, majority of food items and difficult food items. Columns 9–13 gives information on the habitual tool variants: age of competent use (including manufacture), manufacture and use, time (in months) between first object exploration and full competence in tool use and manufacture, age of proficient tool use (incl. manufacture), short description of tool variant, study site from which ontogenetic data originates, tool type: U, use; M, manufacture; S, tool set. The last two columns provide references for tool data and other developmental information. NC crows, New Caledonian crows; B. dolphins, bottlenose dolphins.)

			start explore		competent feeding w/o tool								reference	
species	sex mat.	wean/ fledge	food	objects	simple	most	complex	competent TU + M	learning period	proficient TU + M	tool variant (site)	study site	type UMS	tool	−tool
sea otters	48	6	1	1–2.5	1–4	*3–4.5*	3–4.5	3–4.5	>2	4.5–5.5	rock hammer	all	TU	[7,22,23]	[7,22]
NC crows	24	6–12	1	1–2	1–2	4	6–12	2–4	>1	12-	non-hooked stick	Mare	TU	[8,9,24]	[8,25,26]
								7	>6	12-	*Pandanus*-wide	Mare	TM	[9,27]	
								?–12	<10	12-	hooked stick	Grand Terre	TM	[28]	
capuchins	55	12	2	1	6	12	12–24[b]	6–24	>5	<24	stick-weapon	Serra Capivara	TU	[29]	[30,31]
								>6–48	>5	<24	stone-dig	Serra Capivara	TU	[29,32]	
								>6–48	>5	>24	stick-probe	Serra Capivara	TM	[29,32]	
								24–48	>24	>48	stone-pound	Serra Capivara	TU	[29,32]	
								24–48	>24	>48	two tools	Serra Capivara	TS	[29]	
								25–30	>24	>30	stone (nuts, etc.)	Tiete	TS	[33]	
								24–48	>24	>24	termite fish	Mamanguape	TU	[34][c]	
chimpanzees	118	60	5	6	24	60	120	24–36	>18	60	ant dip	Bossou	TM	[35]	[36–40]
								29	>23	>36	ant fish	Mahale M	TM	[41]	
								30–66	>24	>120	termite fish	Gombe	TM	[42]	
								36	>30	>120	leaf chew/fold	Bossou	TM	[43]	
								36–42	>30	96–120	nut cracking	Bossou	TS	[44,45]	
								42	>36	>96	leaf folding	Bossou	TM	[44]	
orangutans	132	84	12	12	18–20	34–36	36[d]	48	>36	120	tree hole	Suaq	TM	[38][e]	[46,47]
								84	>72	120	*Neesia*	Suaq	TM		[38,39]
B. dolphins	120	36–96	1	1	3	6	60-[f]	20	>20	>36	sponge	Shark Bay	TM	[12,48,49]	[12,49–51]
humans	198	24–30	6	1	6	24	180	18	>17	300	out-of-reach	Hunter–gatherers	TU	[52]	[37,39,53,54]

[a]In case of doubt or sex differences, the younger alternative was used.

[b]Feeding *Luehea candida* by *Cebus capuchinus* (slower life history).

[c]Limited observational data.

[d]Feeding on water or honey from tree holes without the use of tools (E. Meulman 2013, unpublished data).

[e]E. Meulman 2013, unpublished data.

[f]Beach hunting (also influenced by body size).

and object-carrying pouches [63], which might contribute to the lack of geographical variation exhibited in terms of presence of tool use—although variation in frequency and preferences exists—and their relatively young age at competence (figure 1). At the other extreme, we have the habitual tool-using bottlenose dolphins that are not well designed for object manipulation, which perhaps explains their small repertoire of tool variants so far [12]. The sponging dolphins are moreover tasked with searching for prey in an entirely new way, where vision and sonar become secondary to the sponge tool use itself [48]. They may even need to inhibit a likely predisposed resistance to put something over the beak and face, which interferes with echolocation and grasping prey. Other phenotypic biases are more subtle. Thumb morphology, for instance, allows for complex object manipulation in capuchins, chimpanzees [64] and precision grip in humans [65], but capuchins initially tend to strike or rub objects, whereas chimpanzees tend to stack them [45,56,66]. Thus, in acquiring nut-cracking skills, capuchins must learn to place a nut on the anvil before striking it, suggesting that striking is more fixed than stacking, whereas the contrary seems to apply to chimpanzees. Actions that are less fixed may therefore require more time to master and perform in a routine fashion than tool variants involving a more fixed action pattern, for which expression seems to be less variable and dependent on ecological contexts and learning opportunities.

3. Experimental evidence: cognition and tool use

The discrepancy between adult and immature tool behaviour described above, which does not seem to be owing to physical size or strength, thus suggests a role for cognitive skills to adjust or overcome predisposed action patterns, or to master behaviours that are not in the inherited repertoire. An ability to innovate, knowledge of object properties and observational learning has been suggested to be important [67]. All of these have been shown to correlate with slow life histories and brain encephalization [68–71]. In this section, we examineevidencefromcaptive studieson problem solving with objects and tools, and consider how studying cognitive underpinnings and developmental change might help us to identify candidate cognitive adaptations underpinning habitual adult tool use.

(a) Adjusting phenotypic biases

If the tool-using action is not in the inherited repertoire, the animal may need to inhibit or change performance of other predisposed actions in that context. The errors described in the

previous section may indicate an inability to inhibit such actions. Work in the laboratory shows that inhibiting so-called 'pre-potent' responses can indeed be a significant hurdle to problem solving in immature humans and mature primates (but see [72]). For example, chimpanzees performance on trap problems reveals that using a tool to rake-in the reward is easier for them than using a tool to push it away, in which they are less successful (see [73] for a review). Looking-time experiments showed that human infants, as young as four months, and mature monkeys are capable of anticipating that a dropped object will not pass through a hidden shelf, as revealed by longer looking when the dropped object is revealed below the shelf rather than resting on top of it [74,75]. However, when the object was dropped behind a screen onto an occluded shelf, both groups show a bias for searching beneath the shelf, perhaps owing to experience inducing an overgeneralized expectation for objects to be located at ground level. Older children (2.5– 3 years) and mature apes show evidence of being able to overcome this bias and search in the correct location [74,76]. In other problem-solving contexts, both monkeys and infants show perseverative reaching (i.e. repeatedly searching in one location) and fail to use action flexibly depending on the context to solve the task [77]. Interpreting the dissociation between positive evidence from looking measures, and negative evidence from action, has generated a good deal of controversy [78]. However, the notion that integration between object knowledge, memory, and planning and executing goal-direct actions requires maturation of the pre-frontal cortex [79] and therefore a period of development, is an interesting one, that invokes the need for further studies. In toddlers, the ability to solve the ramp task, in which they need to open a door to locate a ball that was rolled down a ramp and should have come to rest in front of a partially obscured wall, has been shown to correlate with success on tasks measuring inhibitory control [80]. There is considerable variation in inhibitory skills across primate species [81]. Investigating how this relates to tool use and problem-solving competence will, therefore, be an interesting question for future work.

Contrasts between species that routinely use tools in the wild with closely related species that do not, can also inform on phenotypic biases. For example, experimental studies comparing tool-using woodpecker finches to the non-tool using but closely related tree finches indicate that both species possess flexible cognitive adaptations considered foundational for tool use [11]. Likewise, both the tool-using New Caledonian crows and the non-tool-using common ravens start off with similar frequencies of object manipulations, considered a precursor for tool use, possibly originating from their shared propensity for food caching. Naive New Caledonian crows do show higher motivation for continued performance

of object combinations, facilitating learning, whereas this decreases over time in common ravens, possibly owing to a higher probability of social interruption for ravens [82]. Such evidence suggests that the cognitive traits underpinning tool use preceded rather than evolved with tool use. Tool use in these species may therefore be better conceived as a manifestation of cognitive traits, rather than a selective force on cognition (see also Discussion).

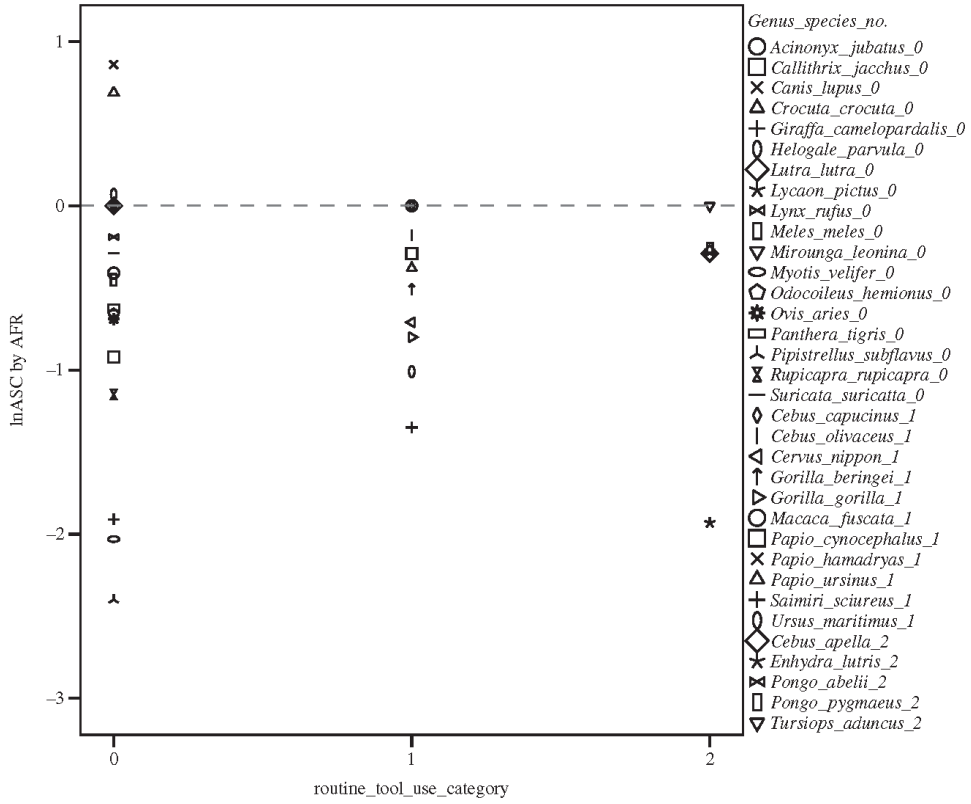

Figure 1 A preliminary dataset including 34 species (Artiodactyla: n = 5, Carnivora: n = 13, Cetacea: n = 1, Chiroptera: n = 2, Primates: n = 13) suggests that most habitual tool users do seem to acquire their skills relatively late during ontogeny compared with other species that were not qualified as habitual tool users by Shumaker et al. [1] (although differences are not significant). Legend numbers refer to tool-use category as displayed on the x-axis. Sea otters appear to be an outlier among the habitual tool users (acquiring their tool use relatively fast); whereas spotted hyaenas and wolves appear to be outliers among the non-routine tool users because they acquire their skills (i.e. hunting skills) relatively late. Data on age at skill competence (ASC) and age at first reproduction (AFR) were taken from Schuppli et al. [55]. Data on routine tool use come from Shumaker et al. [1].

(b) Problem solving with and without tools

Studies exploring the relationship between problem solving and executive control (e.g. inhibition) can not only be explored from onto-and phylogenetic perspectives, but also by comparing mature performance, focusing on the influence of including a tool relative to performing a similar task without a tool. Trap problems, for example, demonstrate that

chimpanzees are more successful in choosing which way to move a reward with one tool than choosing one of two pre-positioned tools. Moving the reward with merely the fingers is easiest of all [83]. Similarly, two-and-a-halfyear old children performed much better on a non-toolusing variant of the trap problem than they did when they had to use a tool (A. M. Seed 2013, unpublished data). Learning to solve a new problem with a tool may be more cognitively demanding, and seemingly small differences in the required action can have large effects on performance. This may be because of demands on executive function, for example, splitting attention between the novel action and the physical task at hand (see [73] for a review). Additionally, reduced visual feedback, such as when the food is hidden or out of reach, or when visual attention is taken away from the movement of the goal (e.g. when focusing on the tool rather than the food reward) may make the acquisition of a new tool-using action more difficult, as revealed by new work on both New Caledonian crows [84] and chimpanzees [85]. For chimpanzees, individuals that had already acquired the solution did not suffer any impairment from the removal of visual feedback, suggesting that feedback is most important during learning.

(c) Innovation and social learning

What is unclear, and contentious, from the pattern of slow, error-prone acquisition of habitual tool use is the extent to which social learning is required. The performance of tool-using animals such as New Caledonian crows and apes, presented with novel multi-step problems in the laboratory, allows individual learning and problem-solving abilities to be isolated from social influence. One approach has been to present naive captive adult apes with the same problems they solve by using tools in the wild. Several problems were solved by these apes without social input. Although this does not preclude the idea that in the wild social influence plays a role in shaping the behaviour, it does falsify any argument that posits a need for social input based solely on the perceived level of difficulty or complexity of the task [86]. Other studies use artificial tasks designed to probe the extents and limits of innovative problem solving. These reveal that both New Caledonian crows and chimpanzees can solve novel problems that involve up to three tools to be used in sequence [87–89], although this does seem to require more practice (see also [66]). Both apes and New Caledonian crows (as well as kea) can also solve problems that involve finding a novel solution, which becomes obsolete after a time, requiring that solution to be abandoned and another to be found [90,91]. The precise cognitive mechanisms behind these impressive problem-solving skills are a

matter of dispute (see [92] for a review). Nevertheless, it is clear that it is within the capability of these species to solve new problems involving unfamiliar materials and using novel behavioural sequences. One point to note is that to date there has been no evidence that tool users outperform non-tool-using relatives in the arena of innovation or problem-solving involving tools (see [93] and [94] for examples of innovation and sequential tool use in non-tool-using rooks). Interestingly, performance in these studies is often characterized by large individual differences, with some experiments showing a minority of individuals completing the most difficult conditions [89,95,96]. Of those solutions to natural problems which require innovations, social influence is likely to reduce intrapopulation variation in tool use. Can developmental studies support this?

4. Developmental evidence for the role of social input

Observational field studies on individual variation within a population provide some of the clearest evidence that social-learning opportunities can have an impact on tool acquisition. Among mammals, nursing young associate more with their mother than with any other individual and she is often more tolerant of immatures than others. A correlation between individual variation in tool use among mothers and offspring (e.g. in terms of time spent using tools, preferences for a certain type or technique, etc.) can be used to provide evidence for vertical transmission. Indeed, variation in percentage of ant-dipping time among chimpanzee mothers at Bossou was shown to correlate positively with ant-dipping time and duration of ant-dipping sessions in offspring, and negatively to infant age of competence and number of dipping errors [35]. A study on termite fishing in chimpanzees at Gombe revealed similar patterns, although here the relationship was not always that straightforward [42]. Preferences for type of prey, method of tool use and foraging tactics strongly correlate between mother and offspring in sea otters and dolphins [7,48]. Juvenile New Caledonian crows show a preference for either Pandanus or stick use, and possibly tool-manufacturing techniques dependent on tool preferences of their parents, although for the latter larger sample sizes are required [27]. Individual variation among parents may also be present in the form of different association patterns affecting the number of social-learning opportunities. Van Schaik et al. [97] demonstrated a strong relationship between tool-use competence and mean female party size in orangutans. An analysis of social networks among tool-using dolphins, showed that after weaning, spongers preferred to associate with other spongers [61], which may be crucial for them to be able to find the best sites for tools and prey. Such social-

learning opportunities may also affect tool repertoires on a wider scale (i.e. at population or species level). For instance, New Caledonian crows have one of the longest known periods of regular extended parental provisioning in birds [25]. Evidence for habitual tool use in orangutans comes from a site inhabiting the densest population [98]. Idem for Goualougo chimpanzees [99], who have a rich tool repertoire including various tool sets [13]. A comparative analysis on emergence of skill acquisition among mammals and birds also indicated an effect of gregariousness, slow conservative development, and post-weaning provisioning and sharing of resources, on age at skill competence [55]. But how do such increased opportunities for social learning serve individual skill acquisition?

Social-learning opportunities can result from the mere presence of other individuals (local-enhancement), the presence of materials manipulated by other individuals (directly by food and tool transfers, or indirectly by stimulus enhancement through artefacts), and models of the complete action (observational learning). We will briefly discuss some indications for the role of these different kinds of input. The presence of other conspecifics, scrounging and/or food transfers are common for most species and behaviours especially at an early age when individuals still depend on their parent(s) for most of their nutritional intake [100]. This facilitates associating the food reward with the tool, which may provide young with a motivation to persist after repeated failure or reduced visual feedback [9,13,44,101]. Delayed or hidden rewards are commonly encountered in natural tool-use settings (see also [101]) and young naive individuals indeed mainly (attempt to) use tools during sessions when their parents also use a tool (e.g. 100% and 62% for Bossou chimpanzees under 5 years, or from 5 to 10 years, respectively; and at least 40% for juvenile New Caledonian crows) [27,35]. In orangutans, also adult tree-hole tool use often seems to be preceded by another conspecific using a tool or engaging in insect foraging (E. Meulman 2013, unpublished data).

With age, tolerance to scrounging and food transfers gradually declines, and infants start to become interested in the tools used by others, as well as attempting to select and manufacture their own tools. Recycled tools contributed to 80% of the termite-fishing tools used by young naive Goualougo chimpanzees and 95% of the Pandanus tools used by two-to three-month old juvenile New Caledonian crows which decreased to only 5% for seven-to nine-month old crows ([9]; C. M. Sanz 2013, personal communication). Counterparts, that is left-overs from the tool-manufacturing process, may be used as well [9,17]. Most of the first self-made tools are dropped (without use) and replaced by tools made by others to obtain the food reward [9,27,42,43]. Such re-use of tools may facilitate learning of how to use these tools and what kind of tool features may be required for the task, especially when visual

feedback is minimal [27,44,101, 102]. Indeed, individuals master tool use, often if not always, before mastering tool manufacture [9,42,44,72,103]. Laboratory work supports the social enhancement of objects used as tools: for example, young New Caledonian crows and capuchins showed a preference for handling objects or tools that had been manipulated by demonstrator individuals [8,104]. Also adult ant-or termite-fishing chimpanzees were more successful if they used tools that had just been abandoned by a previous user, rather than self-selected tools [105,106]. An exception appears to be bottlenose dolphins, where calves must always obtain their own sponge tools and have not been observed using a sponge that was previously used by another (J. Mann 2013, unpublished data). Also orangutans rarely re-use tools, probably owing to low levels of social tolerance and arboreal settings [107]. Reuse of tools does seem to occur more often for tool variants that require specific materials and modifications in chimpanzees [8,13,101], or the use of tool sets in primates [108].

Naive individuals may additionally learn through observation of a more experienced or proficient individual [44,109]. Time observing is negatively correlated with the age of successful termite fishing (Gombe [110]) and ant dipping (Bossou [35]) among chimpanzees and positively correlated to nut-cracking proficiency among brown capuchins in Tiete National Park, Brazil [109]. Dolphin calves have ample opportunity to observe their mothers using sponge tools and are attracted to the fish catches by older individuals [48]. Preliminary data on orangutans suggest that there is more object play or feeding attempts after infants watched another individual using a tool (E. Meulman 2013, unpublished data). High-fidelity action copying may provide human children with an alternative and quick route to obtain a material culture [111,112]. In fact, human children are rarely successful at making functional tools without a demonstrator until they are age 7 or older [72]. Although captive studies on apes do suggest that apes are capable of using both sources of information, results are mixed (see [113] for a review) and it is hard to know from observational studies what aspect of the action is attended to and affects learning, that is action imitation or observational learning of object affordances. How such different strategies of observational learning in particular, and socially facilitated learning in general, may impact speed and reliability of the transmission process may provide us with an interesting scope for future experimental studies (see [104,114]).

In conclusion, the observation that rates of scrounging, object play, feeding attempts, and food and tool transfers, and watching decline with age (and possibly competence) in most, if not all, species [35,100,109], seems to be a further indication for socially facilitated learning during the ontogeny of habitual tool users. Additionally, some rare incidences of

opportunity teaching have been reported for chimpanzees [35,115]. Habitual tool users thus seem to profit from socially scaffolded learning environments that facilitate education by master-apprenticeship [27,116].

5. Discussion

To date, habitual tool use and the degree to which it reflects flexible cognitive adaptations remains a controversial and unresolved issue. A review of longitudinal and experimental studies on the ontogeny of tool use and cognition does, however, shed some light on this notorious problem. First, both field and captive studies demonstrate that young animals of habitual tool-using species make a series of errors during (initial) tool-using attempts, which improve over time. These errors help to identify difficult elements of the tool behaviour and illustrate when animals might need to adjust and/or inhibit predisposed action patterns for the correct tool use (e.g. the capuchin's tendency to rub objects or dolphins 'blinding' themselves by carrying a sponge). Second, some tool-mediated behaviours emerge relatively late in development compared with most, but not all, other foraging skills that do not involve tools (table 1 and figure 1). Initial attempts suggest that physical strength does not explain the late age of competence, but that these tool-assisted behaviours may be cognitively demanding instead. Captive studies indeed provide support for the idea that inhibiting pre-potent responses and using tools to solve problems (rather than using hand or beak) are cognitively demanding activities that improve over development. To date there is no evidence for cognitive specializations in tool-using species compared to non-tool-using relatives (see [93]), but there has been little exploration of differences in domain-general executive functions such as inhibition and attention between species. Third, ecological-and social-learning opportunities during the early stages of development appear to play an important role in determining later skill levels and thus individual and geographical variation [10,61]. Variation among adults moreover indicates that tool performance is not simply a matter of brain maturation but also (social-) learning opportunities. Social transmission seems to be mainly vertical, through association, tool recycling, food and tool transfers, and watching. Other modes of transmission, although not predominant, might nevertheless be crucial as for example suggested by the finding that habitual tool use only occurs in populations with increased opportunities for social learning owing to enhanced social tolerance [97], prolonged parental feeding or association [25], exposure to artefacts [108] and/or perhaps rare cases of

opportunity teaching [35,115]. Re-use of tools may be important for the accumulation of technological complexity [13,108].

The different lines of evidence illustrate two extremes related to the evolution of tool use in animals. At one extreme, only minimal cognitive and social inputs are necessary for the occurrence of tool use, typically because of the presence of an inherent bias to manipulate objects in the first place. The studies on woodpecker finches and North American badgers are good examples, showing that expression of tool innovations mainly depends on ecological factors [10,62] and when flexible cognitive strategies are involved, they appear to be domain-general learning mechanisms shared with non-tool-using relatives [11]. Practice can nevertheless be important, especially for more intermediate forms (e.g. sea otters who specialize[2] in using rocks to open snails are more efficient than non-specialists [23]). At another extreme, more flexible cognition may be required to come up with innovations that deviate from more pre-potent action patterns and additionally require long periods of individual practice and social input to use the tool more systematically and habitually. Dolphins, for instance, are not 'built' for manipulative tool use, but can readily integrate acoustic and visual inputs to represent objects [117,118], and use their cognitive ability to solve problems with tools in laboratory and field, at least when the conditions call for it. Calves of bottlenose dolphins spend thousands of hours observing maternal tool use before the first instances of tool use are observed [48]. Even then, it still takes them decades to show peak proficiency, that is, if they adopt the skill at all [58]. All the females that do are specialists [48].

For both extremes, there are indications that tool use may be better viewed as a possible manifestation (or by-product) of flexible cognitive abilities rather than acting as a selective force on intelligence itself (see also [119]). Note, however, that tool use may just be one among many other possible 'tool-free' manifestations of general intelligence (i.e. one extreme, such as habitual tool users) and, hence, not all tool users need to be characterized by enhanced intelligence (i.e. other extreme, relatively inflexible tool 'specialists'). Although for the moment, this remains speculative and needs further confirmation, this indeed would explain the flexible cognitive traits that are found in wild tool-using woodpecker finches, New Caledonian crows, robust capuchins, and chimpanzees, as well as their non-habitual tool-using (at least in the wild) close relatives: tree finches, common ravens and rooks, gracile

[2] Tool use as foraging specialization is considered in this manuscript the usage of a foraging tool for 50% of an animal's foraging-time budget.

capuchins and bonobos [10,82,93]. Second, it is in line with findings from previous studies that revealed a positive correlation between tool use (or niche complexity), social learning, innovation, brain size, slow life-history pace and general (or cultural) intelligence, whereas the different traits by themselves cannot account for the diversity of tool use across taxa [30,68,71,120]. Finally, it is consistent with previously proposed evolutionary factors for tool use in that: (i) predispositions and/or intelligence stimulate the occurrence of tool innovations; (ii) ecological factors provide opportunities for practice and determine the usefulness of tool innovations;

(iii) intelligence stimulates a more flexible integration of such tool innovations in the behavioural repertoire, that are subsequently more likely to be socially transmitted and thus to be retained within the population's repertoire; especially (iv) in socially scaffolded learning environments [108,121,122].

In summary, evidence from observational and experimental studies indicate that using tools seems to be more cognitively demanding than performing the same behaviour by beak or hand, and flexible use seems to coincide with plasticity during development. Whereas the first conclusion applies to tool use, the latter may apply to 'tool-free' behaviours as well and hence certain 'tool-free' behaviours may thus very well be more cognitively demanding than certain behaviours involving tool use. Although the term 'habitual tool use' is often used to imply socially learned and flexible tool use, this inference could be incorrect if based on geographical variation alone. Social learning is unlikely to be limited to cases of habitual of discarded tools, food, conspecifics or material), and for tool use [5,6], and socially acquired tool use may still be rather controlled investigation of, for example, the ontogeny of inflexible in it is expression (i.e. no adjusting of the behaviour manipulative ability and cognitive–perceptual skills using to a slightly modified task, such as the use of rocks by sea object, tool, or non-object-mediated tasks (e.g. looking-time otters). Flexible tool use may still be based on cognitive strategies experiments). Such experimental work may help uncover that do not require social input (e.g. woodpecker finches) and the link between tool use and specific cognitive processes relying on one snapshot of a population is unrealistic and (e.g. executive control). Future work aimed at pinpointing misses the individual variation. Finally, the variation within the cognitive skills required for tool use could moreover and among routine rather than habitual tool users across fora-help identify candidates for adaptive change in habitual ging and non-foraging contexts requires further study. After tool users. Potential fitness effects of tool use, as well as all, human tool use is also of a customary rather than habitual how these may be influenced by personality traits (e.g. bold-nature. To study social

and cognitive influences on tool use, ness, neophilia and sociability) [123], are currently still developmental approaches and fitness outcomes, thus, may be largely unexplored study themes. Examination of how cognimore fruitful than the focus on geographical differences. Only tive traits and foraging strategies are manifested differently then we can begin to unravel how the ability for tool use evolved among individuals, according to varying conditions, how and relates to cognitive evolution and cumulative technology they change during development and affect fitness are essenand culture (see also [95]). tial for understanding the adaptive significance of such traits

(a) Considerations for future work

Investigation on the ontogeny and adaptive function of tool use in animals with slow life histories, including humans, is a considerable enterprise. While field studies reveal much about the social and ecological circumstances that favour tool use, laboratory experiments (for some species) are ideal for understanding intrinsic mechanisms and manipulating specific extrinsic factors (e.g. social exposure to a task). Implementing
new technological advances in both lines of work may provide us with further insights. Filming with remote
cameras can reveal more details about object play, foraging efficiency and tool-use acquisition (including errors) that are either rarely seen by field observers or difficult to quantify in situ. Field experiments can help elucidate the importance of ecological factors and learning opportunities in more natural settings (e.g. presence of raw material, or terrestrial versus arboreal settings). Experiments in captive settings are needed to account for social and ecological influences (presence of discarded tools, food, conspecifics or material), and for
controlled investigation of, for example, the ontogeny of manipulative ability and cognitive–perceptual skills using object, tool, or non-object-mediated tasks (e.g. looking-time experiments). Such experimental work may help uncover the link between tool use and specific cognitive processes (e.g. executive control). Future work aimed at pinpointing the cognitive skills required for tool use could moreover help identify candidates for adaptive change in habitual tool users. Potential fitness effects of tool use, as well as how these may be influenced by personality traits (e.g. boldness, neophilia and sociability) [123], are currently still largely unexplored study themes. Examination of how cognitive traits and foraging strategies are manifested differently among individuals, according to varying conditions, how they change during development and affect fitness are essential for understanding the adaptive

significance of such traits [95]. A broader comparative approach including routine but non-habitual and/or non-subsistence tool use and 'tool-free'
skills, is furthermore needed to relate the adaptive function of tool use to other foraging strategies and other behavioural contexts. Although we have a long way to go in determining what factors, including cognitive, shaped inter- and intraspecific variation in tool use, ontogenetic research is a most promising approach [18,21].

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CHAPTER 6

Flexible tool use and its acquisition in wild Sumatran orangutans, *Pongo abelii*

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Abstract

Semi-free and captive orangutans are known to be accomplished tool users, but in the wild routine and flexible tool use remains limited to only a few populations. Although this pattern in itself seems to suggest flexibility rather than innate mechanisms underpinning the behavior, such claims are controversial. Here we report the first data on the ontogeny of tree-hole and *Neesia* tool use in wild Sumatran orangutans (*Pongo abelii*), to evaluate to what extent these forms of technology are learned rather than reflecting genetically based predispositions. Observational data and data on tool features were collected at Suaq Balimbing, Sumatra, from 1994-1999 and 2007-2011. The results indicate flexible tool use. Although immatures as young as circa five years of age began to make and use tools, they achieved adult-levels of competence in selecting, modifying, and successfully using tools several years later, i.e. well after weaning, and sometimes around adulthood. Observed sex differences were not directly associated with tool competence. Surprisingly often for a semi-solitary species, tool use among immatures took place in a socially scaffolded environment. We conclude that genetically based predispositions may explain the universal incidental use of tools in orangutans. However, the routine use of both tree-hole and *Neesia* tools, which are flexibly applied, highly localized in the wild, influenced by social-learning opportunities, and take a long time to learn, suggests that these are cognitively demanding activities underpinned by extensive learning.

Keywords
Orangutans, Flexible tool use, Ontogeny, Social learning, Cognition

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Introduction

Tool use, defined here as "the manipulation of a detached object (the tool) to create a change in another object'' (see also Parker and Gibson 1977; Meulman, Sanz et al. 2012), has traditionally been associated with advanced cognitive abilities (see for example Dewsbury 2000; Seed and Byrne 2010). However, some have argued that these demands are overrated (Shumaker, Walkup et al. 2011). These contradictory opinions may have much to do with the kinds of organisms that engage in tool use and the extent to which tool-assisted behaviors are developmentally canalized ('instinctive') (Call 2013), as well as whether tools are merely used or also made. Documenting the ontogenetic route to skill acquisition may, therefore, be critical to identify the cognitive underpinnings underlying tool use (Byrne 1995; Meulman, Seed et al. 2013). Orangutans are particularly interesting because of their diversity in especially routine tool use (van Schaik and Knott 2001). The study of routine tool use and its acquisition in wild orangutan may therefore provide us with more insight in the cognitive demands associated with tool-assisted foraging in wild orangutans, and how this may relate to the variation they show across populations, contexts, and relative to other species with routine tool use.

A recent review on ontogenetic studies performed on habitual (i.e. behaviour that occurs repeatedly in several individuals, consistent with some degree of social transmission; *sensu* Whiten, Goodall et al. 1999, p. 682) tool users in the wild, such as chimpanzees, capuchins, New Caledonian crows, sea otters, bottlenose dolphins and humans, revealed

surprisingly similar routes of tool acquisition across species, with learning being more lengthy and socially scaffolded as tool-assisted skills deviate more from the more developmentally canalized species-specific action patterns (Meulman, Seed et al. 2013). The ontogenetic studies also showed that social transmission - even in the more gregarious species - mainly occurs vertically (i.e. via the mother), especially through enhancement learning induced by the presence of other individuals and artifacts. This may explain the cultural patterns found in the wild.

The present study of tool ontogeny is the first in its kind for wild orangutan tool use. Aside from one brief qualitative account by van Noordwijk and van Schaik (2005), who mention that orangutans start using tree-hole tools between four to six years of age and *Neesia* tools at circa seven years of age, only anecdotal accounts exist about different forms of object manipulation exhibited by orangutans (Lethmate 1976; Lethmate 1977; Lethmate 1977; Parker and Gibson 1977; Lethmate 1982; Torigoe 1985). Bard (1995) described the ontogeny of object manipulation by captive orangutans in more detail, but unfortunately observed no incidences of tool use as defined here (which she refers to as "traditional forms of tool use"). She concluded that whereas complex sensorimotor manipulations were observed in wild orangutans as young as three years of age they tend to use these to travel efficiently and productively, whereas laboratory orangutans appear to use these to manipulate (in)animate objects. However, as Bard briefly mentioned as well, the flexible and routine use of foraging tools by the orangutans in Suaq Balimbing indicates that this discrepancy is not as clear cut as one might think. Hence, the question remains to what extent orangutans use their capacity for complex sensorimotor interactions for tool-assisted foraging, and in how far this can explain their ontogenetic pathway toward tool acquisition.

Orangutans have been shown to be accomplished tool users, especially when kept in captive or semi-free conditions (Rijksen 1978; Beck 1980; Galdikas 1982; Herrmann, Wobber et al. 2008; Bentley-Condit and Smith 2010; Shumaker, Walkup et al. 2011). Wild orangutans also possess an impressive repertoire of tool behaviors (Meulman and van Schaik 2013), but routine use of tools is limited to only a few wild populations, where it is exhibited in the form of tree-hole or *Neesia* tool use (van Schaik and Knott 2001; van Schaik, Fox et al. 2003; Meulman and van Schaik 2013). Tree-hole tool use refers to the extraction of social insects or their products from tree holes. *Neesia* tools are used to extract seeds from the protected fruits of *Neesia sp.*. These are big fruits (ca. 15-25 by 10-15 cm), whose calorie-rich seeds are encapsulated in a tough woody husk. The husk dehisces, but the seeds are embedded in a bed of irritating "fiberglass-like" hairs (Knott 1999, p. 80-153). The large adult males may break

open the undehisced fruits with force, but the other orangutans wait until fruits dehisce and use tools to get access to the then exposed seeds within the fissures while avoiding direct contact with the fruit's stinging hairs.

The two types of tool use have been associated with flexible tool manufacture (i.e. adjusting tool features to the task at hand; see van Schaik, Fox et al. 1996), which is considered to be cognitively demanding (Call 2013). However, in contrast to chimpanzees, the use of tool sets - which may be considered even more cognitively challenging because it involves multiple tools (Sanz and Morgan 2010) - is absent in wild orangutans (Meulman, Sanz et al. 2012).

In this study, we attempted to evaluate how the findings from studies in other habitually tool-using species in the wild and of captive orangutans relate to the acquisition of tree-hole and *Neesia* tool use in wild orangutans, and what this may tell us about the cognitive demands of wild orangutan tool use. We hypothesize that flexible tool manufacture is cognitively demanding and will therefore take a long time to learn. Since orangutans assume a semi-independent life after weaning, we therefore predict a late age of skill competence, around the time of weaning. We start with assessing flexibility in tool use by comparing adult tool features and usage patterns between the two types of tool use (i.e. tree-hole and *Neesia* tool use) and between separate events within tasks (referred to as tool sessions). We first focus on adults to have a point of reference for potential age effects. Differences with age, as indicators for the need for learning, were tested within tasks (to control for the task effect) by examining tool use and manufacture longitudinally over age, as well as cross-sectionally by comparing three age classes: dependents, weaned immatures, and adults. Finally, we assessed the presence of social cues in each tool-use event to infer the importance of socially facilitated learning.

The results confirm that tree-hole and *Neesia* tool use is flexible, habitual, takes a long time to learn and requires social inputs, which suggests it is cognitively demanding, which is in agreement with findings from other habitual tool users.

Methods

Study area

The study area, Suaq Balimbing, is located in the Kluet region of the Leuser Ecosystem, near Sumatra's west coast, in the south of Aceh, Indonesia. The site experiences

the usual climate for the region of two wetter and two drier periods. A gradual transition of four major habitat types can be found. From west to east, these include: tall riverine forest near the Krueng Lembang river, regularly flooded back swamps with irregular and open forest, more closed-canopy peat swamp forest, and finally mixed dipterocarp hill forest. In 1993, a circa 460 ha study site (camp at 03°04'N, 97°26'E) was established and data have been collected from 1994 until 1999, after which the study site had to be left due to civil unrest (Singleton and van Schaik 2001; van Schaik 2004). The site was re-established in May 2007, resulting in the routine following of orangutans again in a now circa 350 ha study grid (camp at 03°02'N, 97°25'E) since August 2007. Research permits were granted by the Indonesian State Ministry of Research and Technology (Ristek), the Indonesian Institute of Sciences (LIPI), the Directorate General of Forest Protection and Nature Conservation (PHKA), the Gunung Leuser National Park (TNGL), the Leuser Ecosystem Management Board (BPKEL), and the Ministry of Home Affairs (Departemen Dalam Negeri).

Data collection

Data on orangutan behavior have been collected from 1994 until 1999 and 2007 until 2011, by *focal animal*, *ad libitum*, and *all occurrences* sampling and through video recordings. Additionally, when possible, tools were sampled, measured and photographed to assess tool features (i.e. length, width, shape, material state, and species of origin). *Ad libitum* data were obtained on details of the initial manufacturing process as well as secondary modifications made afterwards. This included feedback (i.e. inspecting the feeding site before making a tool) and effort (i.e. moving at least 2 meters from the feeding spot to obtain a tool) and whether or not the tool was obtained from the feeding tree. Data on usage patterns involved durations and number of tools used, how tools were held and used, species of feeding tree, whether tools/fruits were parked or transported and left behind or not, whether food was obtained in the end (referred to as success) and whether there was also some foraging without tools during the session. Definitions for behavioral categories mentioned in this manuscript can be found in Table 1. Full details on the methods and definitions of the behavioral categories, are provided at: www.aim.uzh.ch/Research/orangutannetwork.html.

Ages of immatures were (unless known) estimated by four observers based on photographs, body size, facial coloring, rates of suckling, percentage of time spent in close association with the mother (0, 2, 10, or 50 meter), and whether or not the immature was sleeping in the same evening nest as the mother, in a self-made nest within 50 meters, or in a self-made nest at more than 50 meters distance from the mother. Individuals aged sixteen or

more were considered adult. Genetic analyses of 45 fecal samples confirmed unique identity for 29 individuals (unpublished data 2012, Corinne Ackermann). Four individuals had obtained double identities in our dataset (1993-1999: n=3, 2007-2011: n=1), and another four concerned individuals that were followed in the old (1993-1999) as well as the more recent (2007-2011) study period. The majority of the individuals (n=63) were, however, not included in this genetic analysis. An overview of the amount of data per year (or season) is given in Table 2. Table 3 shows an overview of the amount of data per tool type and age-sex class.

Table 1 Definitions of behavioral categories used specifically for this study

Behavior	**Definition**
Peer	Close range watching of another conspecific at a maximum distance of two meters for at least 5 seconds.
Scrounge	Any attempt to obtain food (or tool) that was initially in possession of another conspecific.
Beg	Outstretched hand to other
Reuse	Using a feeding patch or tool that was used by a conspecific less than one hour before.
Follow	Follow a conspecific to a foraging site (used at most 1 hour before)
Try-feeding	Any attempt to feed on an item without properly ingesting it.
Object play	Repetitively interacting with an object seemingly without any obvious purpose.
Tool session	A foraging bout in which one or more tools were used to collect food from a single foraging location (i.e. 1 fruit tree patch, 1 treehole)
Tree patch	Foraging trees of the same species located within a radius of 10m from each other
Tool session	Entire foraging bout in which a tool was used
Feedback	Arrive at feeding site (tree hole or *Neesia* sp. tree at the height at which fruits are growing)
Effort	before obtaining a tool
Straight	Move at least 2 meters away from the spot at which the tool is used first, to obtain the tool
	Without curve or sidebranches

Statistical analyses

To calculate (tree-hole) observation times we summed up the total activity time recorded for each individual during a follow day. On an average follow day (from nest-to-nest) this would start with the individual becoming visibly active at the morning nest and end when no activity could be recorded anymore after the orangutan lay down in the night nest. Partial days were also included. For *Neesia* tool use, observation time was calculated applying similar rules, but based only on the months in which at least one individual was observed foraging on *Neesia*

Table 2 Overview tool data per year (/season)

Tree-hole tool use				
Year	*Months*	*ObsHrs*	*TS*	*TU*
1994	6-12	1463.9	14	8
1995	1-11	3879.8	22	5
1996	1-12	2281.6	22	5
1997	2-11	2152.9	24	6
1998	1-8	2122.6	23	5
1999	2-7	1907.7	27	3
2007	8-12	945.3	11	3
2008	2-11	1334.9	14	8
2009	1-3	635.5	14	4
2010	11-12	430.9	10	2
2011	1-7	1214.6	15	7
Total		18369.6	196	56

***Neesia* tool use**				
Year	*Months*	*ObsHrs*	*TS*	*TU*
1995	2-4	1158.3	13	6
1996	9	56.8	8	1
1998	2-5	903.7	16	9
1999	2-7	1558.9	27	20
2007-08	12-5	1043.6	14	7
2009	3	90.9	8	1
2010-11	12-4	1114.4	14	5
Total		5926.5	100	49

Notes

TS=Tool session, TU=Tool use, ObsHrs= Observation hours

Table 3 Overview tool data per age/sex class

Sex	**AgeClass**	**Age**	**# Ind.**	**ObsHrs**	**ObsHrs**	**TS (T)**	**TS (N)**	**TU (T)**	**TU (N)**
Female	Dependent	5-6	2	216	65	5	0	5	0
Female	Dependent	7-8	3	410	108	10	1	17	1
Female	Dependent	9-10	1	70	70	0	1	0	1
Subtotal Female	*Dependent*	*5-10*	4	*696*	*243*	*15*	*2*	*22*	*2*
Female	Weaned Imm.	9-10	7	979	497	19	11	55	24
Female	Weaned Imm.	11-15	6	12895	9948	11	4	21	6
Subtotal Female	*Weaned Imm.*	*9-15*	10	*13874*	*10446*	*30*	*15*	*76*	*30*
Female	Adults	16+	24	9303	2483	81	50	131	104
Total Female	*All*	*6-17*	34	*23873*	*13173*	*126*	*67*	*229*	*136*
Male	Dependent	0-4	8	18781	10292	2	0	4	0
Male	Dependent	5-6	6	8884	2936	3	0	7	0
Male	Dependent	7-8	5	931	458	0	2	0	6
Subtotal Male	*Dependent*	*3-8*	12	*28596*	*13686*	*5*	*2*	*11*	*6*
Male	Weaned Imm.	7-8	2	1271	1185	0	0	0	0
Male	Weaned Imm.	9-10	4	938	0	0	0	0	0
Male	Weaned Imm.	11-15	5	2689	468	0	2	0	2
Subtotal Male	*Weaned Imm.*	*7-15*	6	*4899*	*1653*	*0*	*2*	*0*	*2*
Male	Adults	16+	41	6052	2175	28	38	42	69
Total Male	*All*	*16+*	*58*	*39547*	*17514*	*33*	*42*	*53*	*77*
Total (F+M)	*Dependent*	*0-9*	*16*	*29292*	*13929*	*20*	*4*	*33*	*8*
Total (F+M)	*Weaned Imm.*	*8-15*	*16*	*18773*	*12099*	*30*	*17*	*76*	*32*
Total (F+M)	*Adults*	*16+*	*65*	*15355*	*4658*	*109*	*88*	*173*	*173*
Total (F+M)	*All*	*0-16+*	*92*	*63420*	*30686*	*159*	*109*	*282*	*213*

Notes

Ind.=Individuals, ObsHrs= Observation hours, TS=Tool sessions, TU= Tool(s) used, (T)=tree-hole tool use, (N)= Neesia tool use, Imm. = immature. Flanged and unflanged adult males were pooled. Some individuals covered multiple age classes.

fruits with a tool. Preferably all months in which *Neesia* sp. was fruiting would have been included, but unfortunately these data were not available for some of the study periods. Tool-session rates were calculated by dividing the total number of tool sessions by the total number of tree-hole or *Neesia* observation hours.

We applied non-parametric statistics due to the small sample sizes, and report exact two-tailed p-values. Logistic regression was used to analyze the effect of observation time to the prevalence of tool use in individuals, and the effect of tool length on some tool features (i.e. peel, straight, dead or live material). The Mann-Whitney U (MWU) test was used for all comparisons involving two groups (i.e. tree-hole compared to *Neesia* tool use, or males compared to females). Age effects were analyzed with the Jonkheere-Terpstra (JT) test for overall longitudinal patterns. "JT values" represent the observed J-T statistic. We did not distinguish in sex of immatures since samples sizes per age group were small, and sex was biased to one or the other direction dependent on the age group (see Table 3). We did, however, test for sex differences among adults to see whether this could have affected our results (see discussion). All analyses were conducted in SPSS version 20.0. R-version 2.15.2 (package car, mlogit, and ggplot2) was used for visualizing the logistic-regression curves.

Results

Effects of observation time

The majority (58.5%) of adult individuals (n=65) were observed to use tools (n=38): 33.8% (n=22) of the adult individuals used tree-hole tools and 43.1% (n=27 out of 62 individuals observed during *Neesia* months) used *Neesia* tools. A logistic regression revealed that observation time had a significant effect on the likelihood that adult individuals were observed to use tools (tree-hole: $X^2(1)=27.76$, $p<0.001$), *Neesia*: ($X^2(1)=19.34$, $p<0.001$); see Figure 1. Thus, focusing on only those adult individuals that were observed for over 100 hours (based on van Schaik, Fox et al. 2003) for tree-hole tool use and 50 hours for *Neesia* tool use, increased the above-mentioned percentages of adult tool use considerably, to 60.7% for tree-hole tool use (n=17/28) and 75.0% for Neesia tool use (n=18/24). To account for this effect of observation time all subsequent results will be expressed as percentages of tools, tool sessions, or ratios of observation time. We therefore conclude that the two forms of tool use among these Suaq orangutans are habitual or even customary [cf. 1].

On average, tree-hole tool use was observed once every 22 days and *Neesia* tool use once every 2-3 days (the average complete follow day contained an average of 687 observation minutes or 11.4 observation hours per nest-to-nest follow [EM unpublished data]). This corresponds to an average tool-use rate of 0.4 (SD=0.8; n=65) tree-hole tool sessions and 3.4 (SD=7.8; n=50) *Neesia* tool sessions per 100 observation hours. This tree-hole tool-use rate is a bit lower than an earlier tool-use rate (i.e. 0.89 tool sessions per 100 hours, in a sample where 23/38=60.5% of the individuals used tools) reported by van Schaik and colleagues (2003).

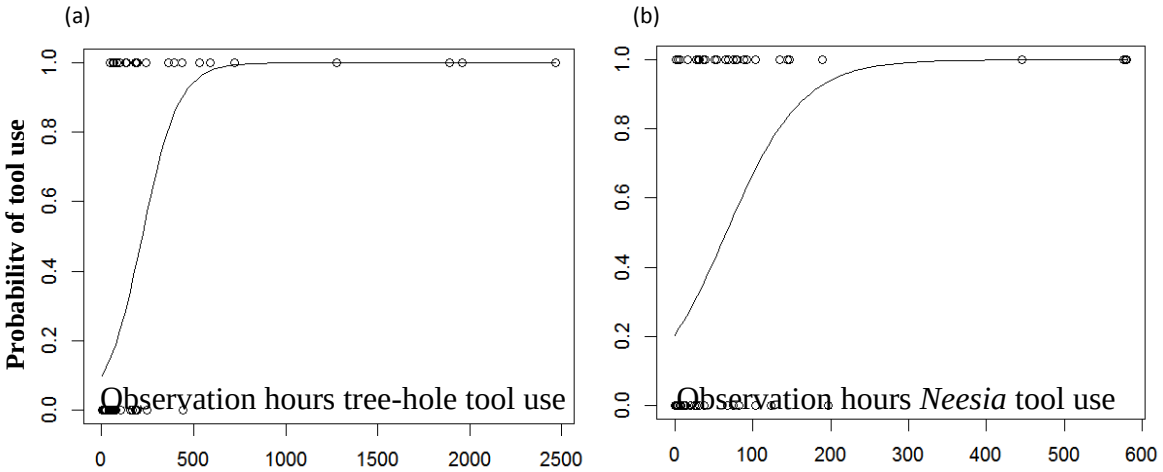

Figure 1 Logistic regression of observation time and manifestation of tool use in adults. Figure (a) represents the data on tree-hole tool use ($X^2(1)=27.76$, $p<0.001$), and Figure (b) the data on Neesia tool use ($X^2(1)=19.34$, $p<0.001$).

Adult patterns

Flexibility according to foraging task

We first examined adult-level tool use so as to be able to place the developmental data into context. Van Schaik and colleagues already demonstrated that tool length and width varied according to foraging task (van Schaik, Fox et al. 1996). This larger data set confirms these earlier indications of flexible tool use, with tree-hole tools (n=171) being significantly longer (n=169; MWU= 1746.0; p< 0.001) and thinner (tree hole: n=162, *Neesia*: n=165; MWU= 1646.5; p< 0.001) than *Neesia* tools. Dividing the two datasets according to study periods with different observers in charge (1994-1999, 2007-2009, and 2010-2011)

demonstrates that these differences are consistent over time (Tree hole: $X^2(2)=0.500$, p=0.975; Neesia: $X^2(2)=4.011$, p=0.135); see Figure 2.

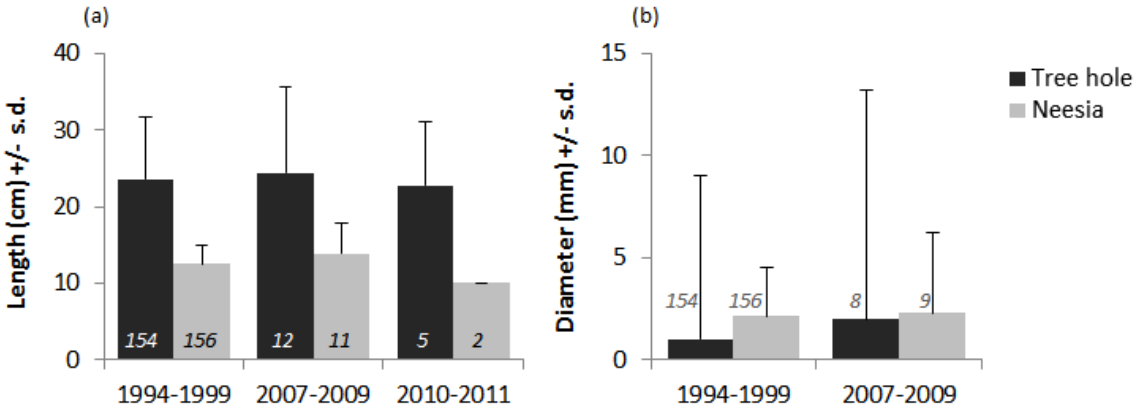

Figure 2 Tool features vary consistently between tasks. Figure (a) shows that tree-hole tools are longer than Neesia tools (MWU=1746.0; p< 0.001). Figure (b) shows that tree-hole tools are thinner than Neesia tools (MWU=1646.5; p< 0.001). Both are consistent over time (no significant differences according to study period). No data on tool diameter were obtained over the third study period.

A further source of possible variability is that tree holes may vary in depth, requiring tool lengths to be adjusted according to the specific tool session. This variation is not expected for *Neesia* tools, because fissures of dehisced *Neesia* fruits are unlikely to differ much per session, although they gradually increase as the season progresses. If anything, we would expect a different tool length according to the mean fruit size of particular crop (and thus season). This expectation is based on census data from van Schaik (unpublished data, 1999), revealing that *Neesia* tools in Tripa (Sumatra) are much smaller than *Neesia* tools in Suaq, as are the fruits (see photo in van Schaik 2004).

Our results indeed confirm the expectations for tree-hole tool lengths (Figure 3), which vary less within sessions (i.e. per tree hole) than overall (93 tools over 37 tool sessions (within); 171 tools overall; MWU= 0.5; p=0.053., whereas this was not the case for *Neesia* tool lengths (168 tools over 4 tool sessions (within); 169 tools overall; MWU= 2.0; p=1.000), see Figure 3.

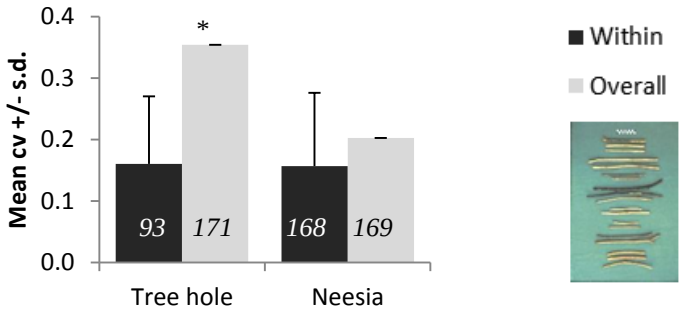

Figure 3 Variation tool length (cm) within and between tasks. The coefficient of variation for tree-hole tool lengths is higher between (overall) than within tasks (MWU= 0.5; p=0.053; n=37 tool sessions) whereas this was not the case for *Neesia* tool lengths (*Neesia*: MWU= 2; p=1.000; n=4 seasons). The numbers in the bars represent the number of tools on which the coefficients of variation were based.

Van Schaik *et al.*, already reported in an earlier study (1996) that the orangutans at Suaq Balimbing manufacture tools by detaching the twig and subsequently removing side twigs and leaves, stripping the bark, fraying tool tip(s), and/or readjusting the length of the tool. In this extended data set we documented these same modifications. Although for most of these processing steps no influence of foraging task was found, as shown in Figure 4, *Neesia* tools were significantly more often peeled (tree-hole: n=171, *Neesia*: n= 179; MWU= 11107.5; p<0.001), straight (tree-hole: n=20, *Neesia*: n=23; MWU= 184.0; p=0.039) and made from living material (tree-hole: n=19; *Neesia*: n=23; MWU= 172.5, p= 0.035) than tree-hole tools. However, a logistic regression revealed that variation in peeling is better explained by variation in tool length, rather than type per se (length: Roa's efficient score statistic (RESS)=58.997, p<0.001; type: RESS= 32.726, p<0.001; interaction length and type: RESS=53.848; p<0.001).

Sex differences

Whereas tool-use rates did not differ significantly between males and females (tree-hole tool use: n=12 females; 16 males; MWU=86.0; p=0.654; *Neesia* tool use: n=10 females; 14 males; MWU=44.0; p=0.130), males used significantly thinner tree-hole tools than females (MWU=1576.0; n=162, p=0.002), whereas the opposite was found for *Neesia* tool widths (MWU= 2044.0; n=165, p<0.001; Figure 5a). Males also used significantly shorter tools than females (tree hole: MWU=2156.5, n=171, p=0.047; Neesia: MWU= 3212.5; n= 169, p=0.590; Figure 5b) and used *Neesia* tools for a significantly shorter duration than females (MWU=

42.5; n=29, p=0.009; Figure 5c). During *Neesia* tool sessions males, additionally, fed significantly more often without a tool after the initial tool use (i.e. just by hand/mouth) than females (*Neesia*: MWU= 52.5; n=28, p=0.041); Figure 5d). These patterns may be explained by the larger body size of especially flanged males and their associated higher frequencies of *Neesia* foraging, especially when fruits are still rather unripe (see discussion).

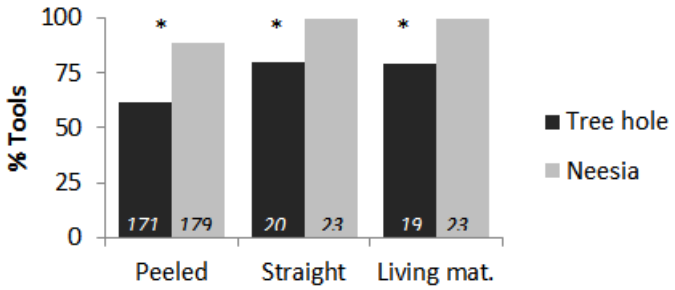

Figure 4 More indications for flexible tool use. The figure illustrates that tree-hole tools are significantly less often peeled (MWU= 11107.5, p<0.001), straight (MWU= 184.000, p=0.039), and made from living material (MWU= 172.5, p= 0.035) than Neesia tools. Numbers in bars represent the total number of tools (100%) on which this data was based.

Age effects

We first examined whether age effects contribute to variation in tool-session rates and patterns of tool use and manufacture observed, without taking into account the degree of social cues present (next section). We analyzed age effects separately for tree-hole and *Neesia* tool use, given that we have just noted that adults adjust their tool use and manufacture according to the type of tools used.

Age of onset

The youngest individuals observed to use tools were four (tree-hole tool use) and five (*Neesia* tool use) years old. However, the first successful tool manufacture and use were observed later, at 5 and 7 years of age, respectively. These results confirm the accounts of age at first observed tool use reported earlier by van Noordwijk and van Schaik (2005). Whereas detailed accounts of tool use and manufacture in these younger individuals are restricted to only very few individuals, they may suffice to characterize some of the challenges facing these immatures (see also Table 4).

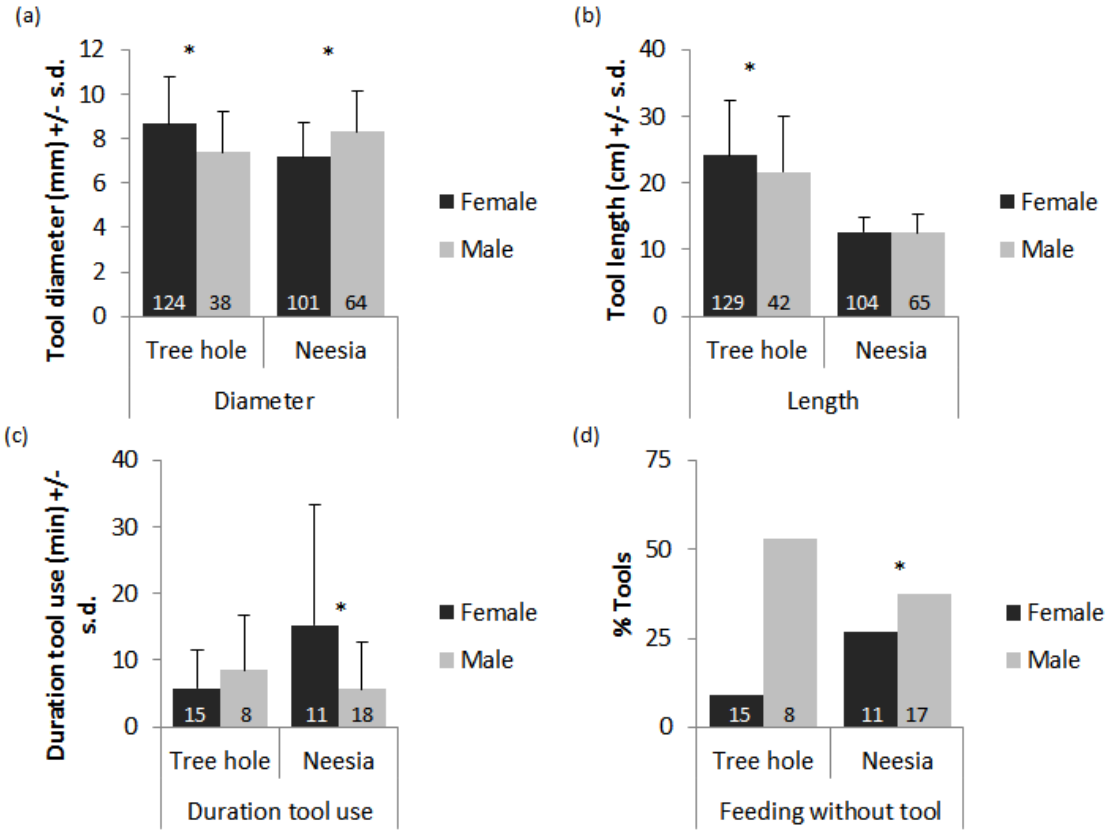

Figure 5 Sex differences in tool use and manufacture. Figure (a) shows the tool diameter in millimetres (tree hole: MWU=1576.0, n=162, p=0.002; Neesia: MWU= 2044.0; n= 165, p<0.001), (b) the tool length in centimetres (tree hole: MWU=2156.5, n=171, p=0.047; Neesia: MWU= 3212.5; n= 169, p=0.590), (c) the duration of tool use in minutes (Tree hole: MWU=55.5; n=23, p=0.789; Neesia: MWU= 42.5; n=29, p=0.009), and (d) the percentages of tools sessions in which was "foraged without tool" after the initial tool use (Tree hole: 53.5; n= 23, p=0.657; Neesia: MWU= 52.5; n=28, p=0.041).

With respect to tree-hole tool use, the first attempts of a four-year-old individual can be characterized as socially triggered (by presence and/or using tools from mother and sister), unsuccessful (the only successful use was at a feeding site at which his mother first fed), and inadequate (poking twigs on a trunk without hole). At five years of age, his tool sessions gradually lasted longer, and resulted in success, but he often started with tools that were extreme in size (too long) and broken in half after some initial feeding attempts. Each tool use was, moreover, followed by some feeding without tool.

Turning to *Neesia* tool use, we lack detailed data on the attempts of a 5-year-old, but earlier reports suggest this was socially triggered and unsuccessful (van Noordwijk and van Schaik 2005). Two seven-year-old individuals were seen to successfully use tools on four occasions. However, for the one individual for whom more detailed data were available, the

tool material seemed rather soft and only a few seeds were obtained, from a fruit that was obtained from her mother and still rather unripe. Subsequent accounts involved nine-year-old individuals (1 female and 1 male, one tool session each). Detailed data for the female clearly indicated success in obtaining seeds from ripe *Neesia* fruits, although she used one tool only very briefly, indicating inefficiency. The various accounts of successful *Neesia* tool use of ten-year-old individuals, however, suggest that successful *Neesia* tool use is indeed generally acquired around 9 years of age.

In sum, initial tool-use attempts appear to be characterized by social triggers (see also next section), very brief use of tools and rather short tool sessions. Tools are, moreover, often inadequate (too soft, dry, or long), and the feeding sites may be unproductive (i.e. no tree hole, unripe fruits, no food), or food can better be obtained without tools. In the next paragraph, we will assess whether these patterns reflect more general longitudinal effects on tool competence, and also over a larger age-range.

Tool use and manufacture

The lack of tool competence observed during initial tool attempts is representative for more general longitudinal differences with age. First of all, tool-use rates gradually increased with age (Tree-hole tool use: $JT(5^3)=970.5$; n=65; p=0.014; *Neesia* tool use: JT(5)=686.5, n=51, p<0.001; see Figure 6). Furthermore older individuals were more likely than younger individuals to engage in tree-hole tool use at successful foraging sites (narrow age classes: JT(5)=708.5, n=57, p=0.005; broad classes: $JT(3^1)=657.0$, n=57, p=0.010; see Figure 7) and their tree-hole tool sessions lasted longer on average (JT(5)=747.0, n=57, p=0.020; JT(3)=706.5, n=57, p=0.014; see Figure 8). These older individuals also used significantly fewer tree-hole tools per unit time in a given session (JT(5)=706.0, n=79, p<0.001; JT(3)=624.0, n=79, p<0.001). For *Neesia* tool use, no such differences were found according to age, perhaps because first tool-use attempts were only observed at later ages. Younger individuals did, however, less often used straight tools for *Neesia* (JT(5)=186.5, n=36, p=0.028; JT(3)=173.0; n=36; p=0.028).

[3] The number between brackets "JT(x)" refers to the number of age classes (x) on which these analyses were based: 5 "narrow age classes" or 3 "broad age classes".

Table 4 Initial tool-use attempts immatures

Name	Age	Sex	Year	TS	Tool	TU_min	TS_min	Manufacture	Success*	Social Trigger	Comments
Tree-hole tool use											
Fredy	4	Male	2008	1	1	0.03	2.00		0	Mother <10m feeding insects without tool	Tool not really used, made from dead material, held in hands, broken in half
Fredy	4	Male	2008	2	2	2.00	2.00		0	no	Trunk without hole, tool held in hands
Fredy	4	Male	2008	3	3	0.50	18.00		1	Peer, beg, tool transfer	No manufacture: used tool from mother
Fredy	4	Male	2008		4	1.00		Peeled	1	Peer, beg, tool transfer	No manufacture: used tool from sister
Fredy	5	Male	2009	4	5	1.50	2.00		0	no	Start feeding ants from trunk without tool, then make tool from dead material, poke with it on trunk (without hole), break tool in half and poke again with both halves simultaneously while no more ant feeding was observed
Fredy	5	Male	2009	5	6	3.63	9.30	Peeled	1	Independently but peered tool use sister few hours before	Exposed tree hole after ripping off bark from trunk. Tool first used then broken in half but then too short, continued feeding by hand.
Fredy	5	Male	2009		7	0.23		Peeled	1		Modified after initial use, continued feeding by hand
Fredy	5	Male	2009		8	2.13		Peeled	1		Extreme size, modified after initial use, continued feeding by mouth
Fredy	5	Male	2009		9	0.68		Peeled	1		Modified after initial use
Fredy	5	Male	2009	6	10	2.02	14.00	Peeled	1?	Peer, beg and co-feed from mother who is feeding termites without tool <2 m away	Too long, after breaking in half not really used, continued feeding by hand
Fredy	5	Male	2009		11	0.08			0		Extreme size (too long), no success, feeding without tool
Neesia tool use											
Ati	5	Female	1995	1	12			Peeled		?	Lacked detailed description
Lilly	7	Female	2008	2	13	2.00	125.00	Peeled, Effort*	1	Peer tool use	Tool from soft material and not straight, fruit from mother, unripe, tool held in hands, only few seeds obtained. First tried without tool.
Peter	7	Male	1999	3	14			Peeled	1?	?	Lacked detailed description
Peter	7	Male	1999	4	15			Peeled	1?	?	Lacked detailed description
Peter	7	Male	1999		16			Peeled	1?		Lacked detailed description
Peter	7	Male	1999		17			Peeled	1?		Lacked detailed description
Peter	7	Male	1999	5	18			Peeled	1?	?	Lacked detailed description
Peter	7	Male	1999		19			Peeled			
Ellie	9	Female	2007	6	20	110.00	110.00	Peeled, "Planning 1"*	1	Local enhancement	Clearly competent in obtaining seeds
Ellie	9	Female	2007		21	0.00	37.00	Peeled	0		Tool not really used
Ellie	9	Female	2007	7	22	14.00	14.00	Peeled, "Planning 2"*	0.5	no	Fruit not entirely opened and fed.
Ati	9	Female	1999	8	23			Peeled		?	
Dolly	9	Male	1999	9	24			Peeled		?	

* Effort: Moved over two meters away from initial feeding spot to obtain tool, "Planning 1": Tool made in *Neesia* tree but before moving up, "Planning 2": Tool taken before arrival but manufactured in Neesia tree, Success: Food obtained with tool. TU_min = Tool use (duration in minutes), TS_min = Tool session (duration in minutes).

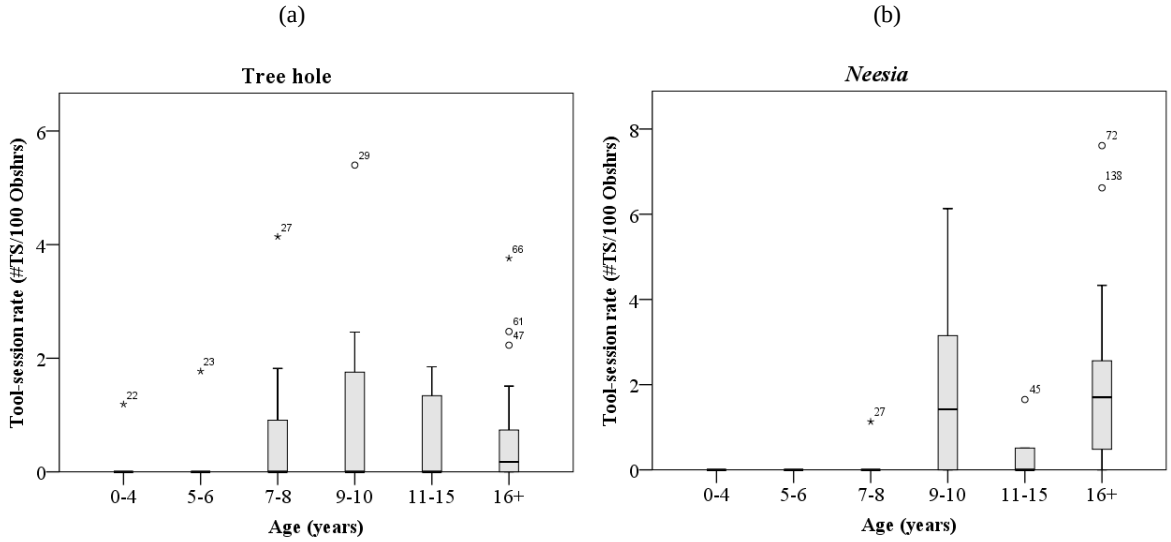

Figure 6 Tool-session rates according to age. Tool-session rates (number of tool sessions per 100 observation hours) increased significantly with age (Tree-hole tool use: JT(6)=970.5; n=65; p=0.014; Neesia tool use: JT(6)=686.5, n=51, p<0.001).

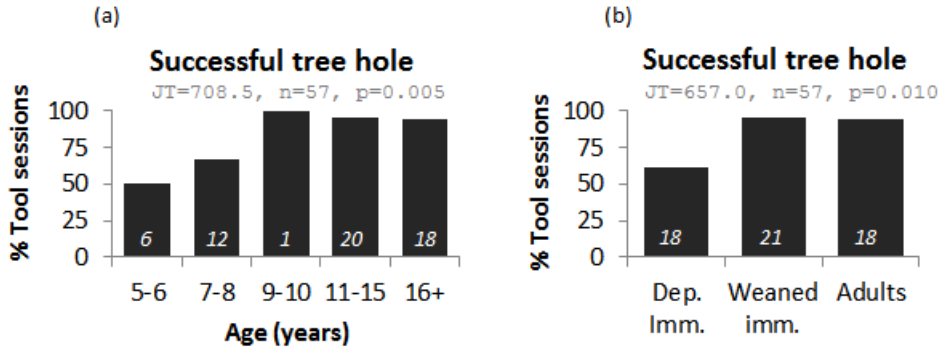

Figure 7 Success in obtaining food at the foraging site increases with age. Figure (a) shows the age effects presented for each two-year age group; Figure (b) the age effect presented for age groups according to their developmental stage (i.e. dependent immature, weaned but immature, or adult).

Social-learning opportunities in tool-use contexts

Van Schaik and colleagues (2003) reported that female clusters differ in tool-use specialization according to their time spent in association (used as a proxy for social-learning opportunities). Although the northern cluster with very limited tool use could not be sampled in this study, we tried to look in more detail at how social-learning opportunities were used by

orangutans, and in particular immatures, to engage in tool-assisted foraging. Figure 9 shows that self-initiated tool use increased with age and that especially older tool users receive interest from conspecifics. Although sample sizes were small, a significant linear age effect was found for the frequencies with which tree-hole (JT(5)= 500.5, n= 59, p= 0.017; JT(3)=448.5, n=59, p=0.017), but not *Neesia* (JT(5)=83.0, n=25, p= 0.499; JT(3)=77.5, n=25, p=0.734) tool sessions were socially triggered. Likewise, linear age trends were found for whether or not conspecifics showed interest in the tree-hole tool user (JT(5)= 875.0, n=59, p<0.001; JT(3)=833.0, n=59, p<0.001). Hence, the combined trend is clear: as animals mature they rely less on the presence of social triggers (in the form of local and stimulus enhancement, scrounging and begging or peering), whereas in turn they receive more interest from younger individuals.

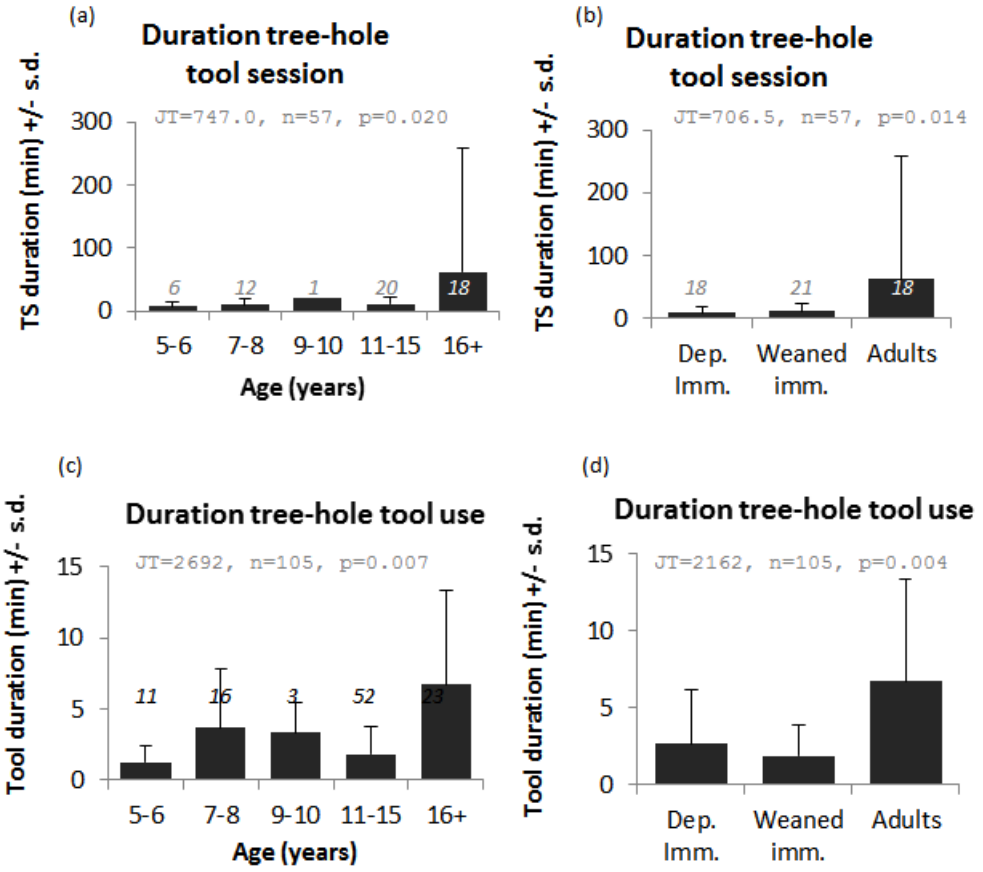

Figure 8 Age and the duration of tool sessions and tool use. On the left (Figure a, c) age effects are presented for two-year age groups. On the right (Figure b, d) the same data is presented combining the age group according to developmental stage (i.e. dependent immature, weaned but immature, or adult).

Discussion

The discovery of tool use in a wide variety of animals (e.g. from ants to elephants) has challenged our traditional perspective on tool use as being cognitively demanding (Shumaker, Walkup et al. 2011). The role of learning and flexibility in use and manufacture is often considered important in this regard (Call 2013). Studies of the ontogeny of tool behavior may be critical to identify such cognitive underpinnings of adult tool use.

The present longitudinal study, based on eleven years of data, is the first in its kind for wild orangutan tool use. Our results confirm earlier findings of routine and flexible use of tree-hole and *Neesia* tools (van Schaik and Knott 2001; van Schaik, Fox et al. 2003), but additionally show that flexible manufacture is additionally expressed in the extent to which tools are peeled, straight and made from living material. Our focus was on the ontogeny of tool use. The results show that initial tool-use attempts of immatures are characterized by the presence of social triggers (through local or stimulus enhancement, peering, begging or scrounging), brief use of tools and short tool sessions, inadequate tool manufacture (too soft, dry, or long), and use on feeding sites that may be unproductive (i.e. no tree hole, unripe fruits, no food) or do not require the use of tools. Although infants start to use tree-hole tools at four years of age and *Neesia* tools at five years of age, they acquire competence in the form of consistent successful tool-assisted foraging only at around 10 years of age for tree-hole and 11-15 years for *Neesia* tool use. Adult levels of proficiency (reflected in the duration of tool use and tool sessions) are not observed before reaching adulthood.

A need for learning

Several lines of evidence, mainly from previous studies, suggest that a genetic predisposition may underpin orangutan tool use, since it seems the most parsimonious explanation for (*i*) the universal prevalence of head covers, branch display, and to some extent nest building in wild orangutans (van Schaik, Ancrenaz et al. 2003; van Schaik, Ancrenaz et al. 2009), (*ii*) the large repertoire of wild orangutan tool use and the multiple, mostly incidental, tool variants reported for each long-term study population (Meulman and van Schaik 2013), and (iii) the proficient tool use by orangutans in captive settings (Bentley-Condit and Smith 2010; Shumaker, Walkup et al. 2011). Weak innovations due to, or in addition to, a genetic predisposition, thus appear enough to trigger the various forms of incidental and universal tool use in wild and captive orangutans.

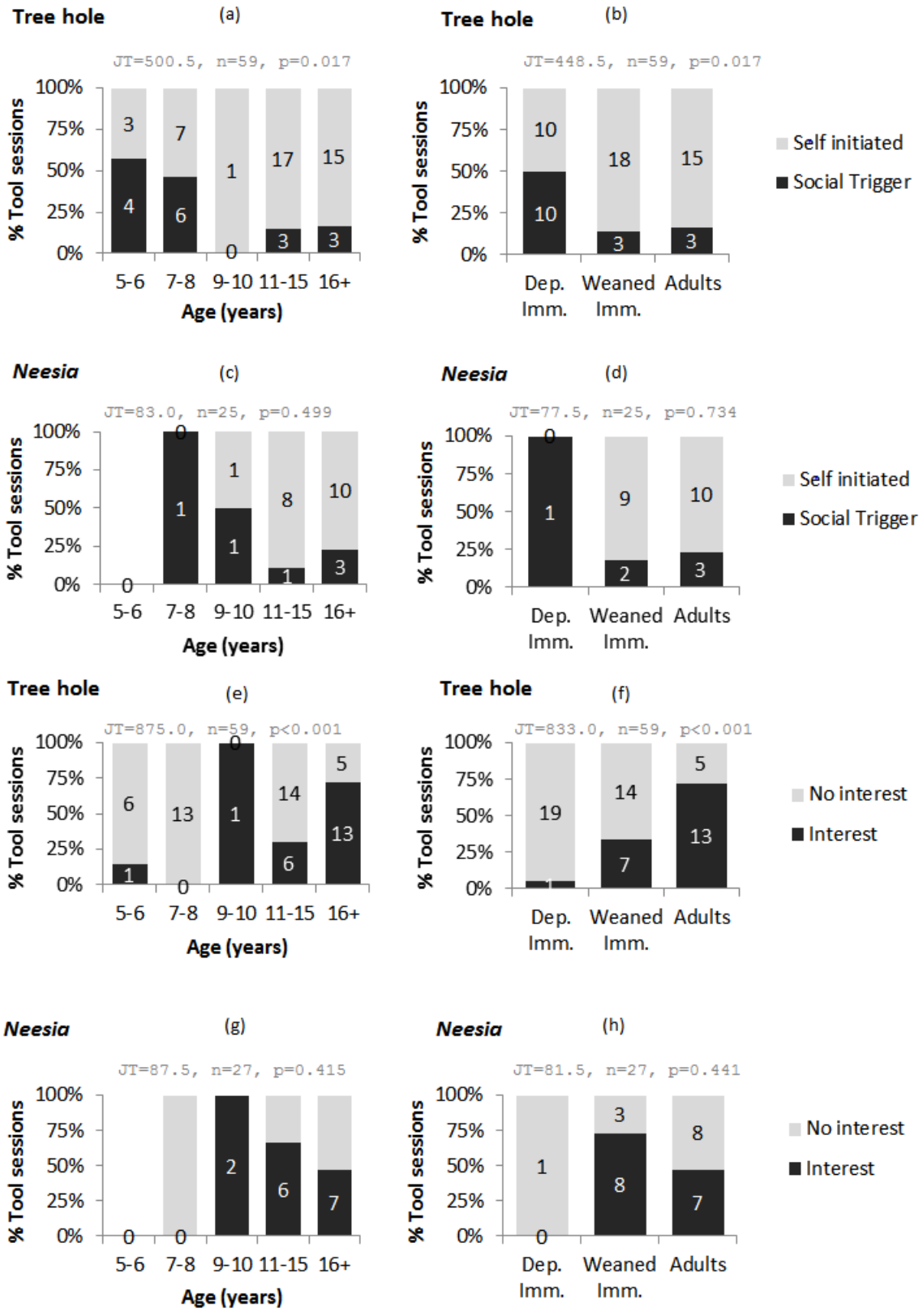

Figure 9 Percentage of tool sessions that were preceded by another conspecific foraging on the same food item (insects or Neesia) at the same feeding site (patch). Tree-hole tool use occurred significantly more often in the presence of social cues for dependents than that it did for weaned and adults (JT=448.5; p=0.017). Since hardly any dependents engaged in Neesia tool use, this effect was not significant for Neesia tool use (JT=77.5; p=0.734).

The patchy geographic incidence of routine extractive tool use [2,3] argues against this position. Observations from the present study do so too. The extractive tool use and manufacture on tree holes and *Neesia* fruits that were focus of this study differ from such probably more hardwired universal and (to lesser extent) incidental forms of tool use in several ways. First, although the later age of onset and sex differences observed for *Neesia* tool use suggest maturation may play a role in handling the large, heavy and tough *Neesia* fruits, exclusively canalized development cannot explain why onset and competence (for especially tree-hole tool use) are acquired much later than other orangutan skills, including nest-building skills or other skills involving complex sensorimotor manipulations (Bard 1995; van Noordwijk and van Schaik 2005; van Noordwijk, Sauren et al. 2009).[4]

Second, variation in tool features in response to varying demands by session for tree-hole, and by season (this study) for *Neesia* tool use, makes a genetically hardwired basis, which is associated with stereotypic and inflexible expression, very unlikely (Call 2013). Instead, the assessment of such tool demands may require trial-and-error learning of relevant features of the tasks (see also Boesch 2013). The observed incidences of "foraging-without-tool" after initial tool use during tool sessions did indeed seem to facilitate such individual practice.

Third, social-learning opportunities appear crucial for learning to recognize foraging opportunities and stimulating tool-use attempts (this study). Orangutans appear to learn rare or complex skills in a social learning-practice cycle (Jaeggi, Dunkel et al. 2010; SF, unpublished data 2009), in which the social component is essential to trigger the practice (see also Gruber, Singleton et al. 2012). The variation within and across populations in social-learning opportunities (van Schaik and Knott 2001; van Schaik, Fox et al. 2003) seems to support this, whereas with canalized development such an influence of social-learning opportunities is unlikely (e.g. Tebbich, Taborsky et al. 2001).

Finally, "mistakes" during initial tool-use attempts, the gradual improvement with age and social-learning opportunities, and the late ages of onset, competence, and proficiency, all suggest that whereas these tool-using skills are indeed difficult to individually acquire, they improve with learning (see also Jaeggi, Dunkel et al. 2010).

[4] Proficiency is more common to be acquired after weaning (van Noordwijk, Sauren et al., 2009)

Implications for orangutan niche complexity and life history

We noted that the late ages of competence and need for a social-learning practice cycle suggest tree-hole and *Neesia* tool use are complex skills. Although comparison of skill complexity relative to other skills, populations or species is associated with problems, the late age of tool competence and need for social learning is in line with what has been reported for other habitually prevalent tool-use skills and tool-using species, even if those are associated with more opportunities for social learning (Meulman, Seed et al. 2013). Other habitual tool users, furthermore, seem to show similar combinations of fixed and flexible mechanisms underlying the development and application of tool-assisted foraging. Moreover, comparative evidence on ontogeny and social-learning opportunities for various skills in orangutans moreover suggests the habitual and flexible use of tree-hole and *Neesia* tools is more cognitively demanding than other skills, with the possible exception of nest building. We therefore conclude that, whereas tool use may be simple, habitually prevalent flexible and geographically variable tool use is cognitively demanding.

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Author Contributions

Conceived and designed the experiments: CvS EM. Performed the experiments: EM SF AP MvN CS CvS. Analyzed the data: EM CvS KI. Contributed reagents/materials/analysis tools: EM SF AP CA SSUA TMS. Wrote the paper: EM CvS.

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CHAPTER 7

Conclusion

The aim of this thesis was to get more insight in the selective pressures and cognitive demands associated with animal tool use, using orangutans as a model species. Chapters 2-6 provide us with five main findings that contribute to our understanding in this regard. First, wild orangutan tool repertoires are richer than we thought, but lag behind in complexity relative to those of chimpanzees (chapter 2). Second, comparative evidence among primates suggest that (semi-) terrestrial lifestyles may have been crucial for the evolution of cumulative hominin technology (chapter 3). Third, in the absence of proactive prosociality, terrestriality leads to more effective tool transfers, which decreases the cognitive threshold for acquiring more complex forms of tool use (chapter 4). Fourth, habitual tool use can only be acquired in socially scaffolded environments and may indeed be considered cognitively demanding as indicated by ontogenetic studies (chapter 5). Sixth, the habitual and flexible tool use observed in wild orangutans is cognitively demanding (chapter 6).

Patterns in orangutans tool use, thus, contribute to our understanding of the evolution of tool use, cognition and humans (see thesis title) in that more terrestrial lifestyles seem to have been crucial for the flourishing of hominin technology, just as they explain why most wild orangutan tool use remains rather simple and incidental. I conclude that since artifacts facilitate information transfer, opportunities for encountering artifacts (such as in the context of tool use) decrease the threshold for cumulative culture and cognitive evolution. Thus, in a way tool use might have made us human after all.

EPILOG

Preserving our vanishing natural and cultural heritage

Geographic variation in orangutan behavior increasingly reveals the intelligent and flexible strategies they exhibit to respond to local enviromental challenges. We have seen in this thesis that tool use is one of these behaviors. Unfortunately, we have also seen that such behavioral flexibilty may take time to learn and requires innovations that are not straightforward to invent and thus rare. Thus, although orangutans are capable of intelligent and flexible behavior in response to local challenges, the rate at which their environment is changing nowadays may be too fast for them (van Schaik 2013).

Habitual flexible wild orangutan tool use has only been found in the form of tree-hole and *Neesia* (seed-extraction) tool use, which has been observed in total in only three locations: Suaq Balimbing, another coastal swamp near Ie Mdamai, ca. 10 km south of Trumon, and along the Krueng Seumayam (3°459510 N, 96°369530 E). Unfortunately, the coastal site near Trumon was logged in 1997, and along the Krueng Seumayam only seven intact *Neesia* trees remained standing until July 1999 (van Schaik and Knott 2001). Selective logging also left its traces at Suaq Balimbing. The data already showed that I observed remarkable fewer tool events during recent years (2007-2011) compared to the first study period (1994-1999) and the negative trend continues. Recent years have seen an increase in selective-logging activities at Suaq Balimbing, resulting in only about 10 *Neesia* trees that were remained standing in the study area, at the start of 2013. If these disturbances continue, it may only take a few more years before tree-hole and *Neesia* tool use are lost from the tool repertoire of most wild orangutans. With such cultural extinction we also lose our window into our past: human evolution. After all, how can we learn about our past, when we have no model system? Anyone familiar with the field of anthropology and palaeontology knows how hard it can be to retrieve knowledge from the ancient past. What better than preserving this opportunity to study our cultural and natural heritage rather than being forced to speculate about it?

Even more tragic are the prospects for the orangutan themselves. Recent studies have shown that even if Sumatran orangutans manage to survive, their lives probably become energetically expensive (Hardus, Lameira et al. 2012) so that densities decline and

populations become non-viable in the already fragmented forest patches (Campbell-Smith, Campbell-Smith et al. 2011; Nater, Arora et al. 2013). Alternatively or in addition, populations are bound to come into conflict with humans more frequently (Campbell-Smith, Campbell-Smith et al. 2011). However, as long as it is not too late we should not and are not allowed to give up hope. Research keeps on providing us with new ideas (Hockings and Humle 2009; Campbell-Smith, Campbell-Smith et al. 2011; Hardus, Lameira et al. 2012; Meijaard, Wich et al. 2012) and as hard as it may seem, determination and patience can take us there, just listen to Dr. Goodall (who keeps on inspiring me).

"*Roots creep underground everywhere and make a firm foundation. Shoots seem very weak, but to reach the light, they can break open brick walls. Imagine that the brick walls are all the problems we have inflicted on our planet. Hundreds of thousands of roots & shoots, hundreds of thousands of young people around the world, can break through these walls. We CAN change the world." - Dr. Jane Goodall.*

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VWO (~highschool); Florens Radewijns College, Raalte; *1993-1999.*

ADDITIONAL COURSES AND CERTIFICATES:

*Animal cognition (*University Neuchatel; 2013); *Topics in Evolutionary Biology, Primate Behavior, comparative methods in evolutionary biology, primate cognition, Microsoft Access, SPSS and R Statistics, Scientific writing, Scientific presentations, Applying for research grants, Research ethics* (Zürich University; 2009 – 2013); *Filming & Editing* (RTV Raalte; 2006); *Fundamentals neuroscience and cognition, Beekeeping, Social Ethology, Measuring Behavior: study setup & statistics* (Utrecht University; 2004); *Radiate Hygiene, level 5b* (Delft University of Technology; 2004); *Psychopathology* (Saxion Hogeschool Enschede; 2002).

Research and Work Experience

Research assistant Primate Station; Zürich University, Anthropological Institute; 2011 – 2012 (dr. J. Burkart).

- Establishing collaborative efforts with zoos
- Conducting pro-sociality experiments (group service test) in *Macaca silenus* at Zoo Parc Overloon

PhD student Evolutionary Biology; Zürich University, Anthropological Institute; 2007 – 2014 (prof. C. van Schaik).

- Thesis title: Wild orangutan tool use. New insights for human evolution
- Project: Culture and Cognition in Orangutan Foraging
- Set up and manage Sumatran field research site & database (Suaq Balimbing, Sumatra, Indonesia)
- Supervise master student and Indonesian bachelor students, local assistants
- Assist teaching block course primate behavior (see teaching experience)

Laboratory technician; Central Military Hospital Utrecht (CMH), Military Psychiatry (MP); 2006 – 2007

- Sole-responsibility for pre-processing blood samples on location for various hormone analyses

M.Sc. student; Utrecht University, Biology; 2004 – 2007 (dr. S. Wich, dr. L. Sterck).

- Project (8.5): Culture in a Bornean Orangutan Population
- Video capture and documentation wild orangutans
- Local representative for managing field research site (Tuanan, Borneo, Indonesia)

M.Sc. student; Utrecht University, Biology; 2007 (dr. S. Reader).

- Project: Modularity in Cognitive Evolution. From mathematical models to the human brain organization

M.Sc. student, Lab.technician; 1) CMH Utrecht, MP; (dr. E. Vermetten & C. de Kloet), 2) Wilhelmina Children Hospital Utrecht, Lab. Psychoneuroimmunology, (prof. C. Heijnen & A. Kavelaars); 2003 – 2004.

- Project (8.5): Posttraumatic stress *(i)* Lebanon veterans, *(ii)* the glucocorticoid receptor, and *(iii)* immunological changes and parameters
- Start collaborative effort with WKZ to do lab. research on PTSD
- Recruit PTSD patients (military) and controls
- Assess neuropsychological interviews and medical treatments

B.Sc. student; UMC St. Radboud Nijmegen, Laboratory for Paediatrics and Neurology; 2002 – 2003 (dr. B. van den Heuvel, M. Löwik, Dr. B. Zantinge).

- Project (8): Mechanisms associated with glomerular ultrafiltration kidney
- Various isolation, extraction and labeling techniques, cell culture, mutation analyses, working with genetically modified organisms.

SIDE JOBS: Until 2004 I have had numerous side jobs in the ICT, administrative and agricultural sector.

VOLUNTARY WORK: *Pongo* Foundation; Local Radio/TV station; Sea turtle project, Local running events (2005 – 2009).

Teaching Experience

Co-director/Lecturer "Primatology, Wildlife, Ecology & Conservation Field School in Kenya"; 1) Rutgers University, Department of Anthropology, 2) National Museums of Kenya Wildlife Service; 2012, 2013 (Prof. J. Harris; Prof. R. Palombit).

- Organize and plan Field School activities, Lecture students about primate behavior and primatology methods, Guide and supervise students to conduct a research project on primate behavior / conservation, etc.

Teaching assistant: Block Course Primate Behavior; Zürich University, Anthropological Institute; 2009 – 2011 (prof. C. van Schaik and dr. J. Burkart).

- Supervise student projects, Lecture Scientific Method, Discuss exercises, Organize materials for lectures and field trip, etc.

PhD student Zürich University, Anthropological Institute; 2007 – 2008
- Train and supervise master students and local assistants
- Outreach program local primary school (independently organized but with support of SOS-OIC)

MSc student Utrecht University, Biology; 2004-2005
- Outreach program for local primary school

Student Secondary Teacher Mathematics; Hogeschool (~College) Windesheim, Zwolle; 1999 – 2000. Practical part at Ichthus College Kampen (underclass havo (pre-college) or vwo (pre-university)).

*Coach soccer team (*girls, 8-10 years old); vvHeino; 1999 – 2000.

Other (Relevant) experience / skills

Language	Dutch (native), English (fluent), German and Indonesian (conversational), French (basic)
Software	Microsoft Office (Access, Excel, PowerPoint, Word), Labview, R, Interact Adobe Premiere Pro, Jmp, SPSS, MatMan, GIS, MapSource
Driving	Driving license B (2000)
Leisure	Filming, sports (volleyball, cycling, jogging, skiing, yoga), travelling Soccer (1988-2004, vvHeino, last 5 years in 1st class country wide)
Personality	Social-minded, Accurate, Perseverative, Passionate, Reliable, Flexible

Funding obtained

2002 UMC Radboud Nijmegen (apartment rent)

2004 University Utrecht - internship abroad (travel, vaccination, permits)

2006 Essent (sponsoring *Pongo* Foundation)

2009 SOS-OIC Sumatran Orangutan Society (educational material outreach program)

2010 Schultz Foundation (travel expenses and conference fees IPS Japan)

2011 Schultz Foundation (half year salary)

2011 Kantonal Funding Zürich (travel expenses and conferences fees GFP and EFP)

2012 Kantonal Funding Zürich (Living expenses Overloon)

Presentations

Meulman, E.J.M.; Schuppli, C.; and van Schaik, C.P. (2013). How Ecology May Affect Orangutan Innovation and Culture. VII Congress of the European Federation for Primatology, University of Antwerp, Belgium.

Schuppli, C.; **Meulman, E.J.M.**; van Noordwijk, M. and van Schaik, C.P. (2013). Do Wild Orangutans Learn From Each Other? Evidence for Observational Learning from Two Populations of Wild Orangutans. VII Congress of the European Federation for Primatology, University of Antwerp, Belgium.

Meulman, E.J.M. (2013). Understanding tool use in orangutans. Ringvorlesung "Knowledge, Communication, Cooperation. Crossing Disciplinary barriers", Zürich, University of Zürich (Uni Zentrum), Switzerland.

Meulman, E.J.M. and van Schaik, C.P. (2012). Acquisition of foraging skills and tool use in wild orangutans. Royal Society International Scientific Seminar "Tool-use as adaptation", London, Kavli Royal Society International Centre, United Kingdom.

Meulman, E.J.M. and van Schaik, C.P. (2011). Terrestriality and the link to prolific technology in orangutans. VI Congress of the European Federation for Primatology / 3rd Iberian Primatological Congress, Almada, Forum Municipal Romeu Correia / Central Library, Portugal.

Meulman, ***E.J.M.***; van Schaik, C.P. (2011). What orangutan tool use can tell us about the evolution of technology. The 12th conference of the Gesellschaft für Primatology, Utrecht University, The Netherlands.

Meulman, ***E.J.M.***; Forss, S.I.F.; Mitra Setia, T.; van Schaik, C.P. (2010). Understanding tool use in orangutans. Why flexible tool use is rare in wild orangutans. International Primatological Society XXIII Congress Kyoto, Japan.

Meulman, ***E.J.M.***; van Schaik, C.P. (2009). Tool use by wild Sumatran orangutans: indications of cultural intelligence. Tool use workshop, Max Planck Institute Leipzig, Germany.

PUBLICATION LIST

PhD:

Meulman, E.J.M., Seed, A.M., Mann, J. (2013). If at first you don't succeed… Studies of ontogeny shed light on the cognitive demands of habitual tool use. Philosophical Transactions of the Royal Society B: Biological Sciences 368, 20130050.

Meulman, E.J.M. and van Schaik, C.P. (2013). Orangutan tool use and the evolution of technology. In Sanz, C., Boesch, C., Call, J. (eds.). Tool Use in Animals: Cognition and Ecology. Cambridge University Press. Ch 9.

Meulman, E. J. M., Sanz, C. M., Visalberghi, E., and van Schaik, C.P. (2012). The role of terrestriality in promoting primate technology. Evolutionary Anthropology 21:58–68.

Sanz, C.M.[5]; ***Meulman, E.J.M.***[5]*;* Morgan, D.B.; Kurtycz, L.; van Schaik, C.P. (in prep.). Prosocial tool transfers in wild great apes? Implications for the evolution of technology. Animal Behavior.

Meulman, E.J.M., Forss, S.I.F., Permana, A.; Schuppli, C., Utami-Atmoko, S. S.; Mitra-Setia, T.; van Noordwijk, M.A., and van Schaik, C.P. (in prep.). Flexible tool use and its acquisition in wild Sumatran orangutans, *Pongo abelii*.

Additional:

Wich, S.; Krützen, M.; Lameira, A.; Nater, A.; Arora, N.; Bastian, M.; ***Meulman, E.***; Morrogh-Bernard, H.; Utami Atmoko, S.; Pamungkas, J.; Perwitasari Farajallah, D.; van Noordwijk, M.; van Schaik, C. (2012). Call cultures in orang-utans? PLoS ONE 7(5): e36180.

Burkart, J. M.; Allon, O. ; Amici, F.; Fichtel C.; Finkenwirth, C.; Heschl, A.; Huber, J.; Isler, K.; Kosonen, Z.; Martins, E.; ***Meulman, E.***; Richiger, R.; Rueth, K.; Spillmann, B.; Wiesendanger, S. & van Schaik, C. P. (subm.) Allomaternal care best predicts proactive prosociality across 15 primate species. Nature.

Kamsi, Mistar; Mukhlisin; ***Meulman, Ellen;*** Singleton, Ian (in prep.). Predation of the Reticulated Python *Python reticulatus* by the King Cobra *Ophiophagus hannah* in Nothern Sumatra. British Herpetological Society Bulletin.

MSc:

De Kloet, C.S.; Vermetten, E.; Bikker, A.; ***Meulman, E.***; Geuze, E.; Kavelaars, A.; Westenberg, H.G.M. and Heijnen, C.J. (2007). Leukocyte glucocorticoid receptor expression and immunoregulation in veterans with and without post-traumatic stress disorder. Molecular Psychiatry 12 (5): 443-453.

Vermetten, E.; ***Meulman, E.***; Francati, V.; Geuze, E. ; de Kloet, C.S.; Unck, F.A.W. (2007). Psychiatrische aandoeningen bij UNIFIL veteranen op de Afdeling Militaire Psychiatrie; een retrospectief dossier onderzoek over de periode 1992-2005. Nederlands Militair Geneeskundig Tijdschrift 60 (1) : 9-15.

[5] The authors wish it to be known that, in their opinion, the first two authors should be regarded as joint First Authors